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Geology

THE HAMILTON FAUNA

A LATE PLIOCENE MAMMALIAN FAUNA FROM THE GRANGE BURN, VICTORIA, AUSTRALIA

WILLIAM D. TURNBULL

AND

ERNEST L. LUNDELIUS, JR.

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THE HAMILTON FAUNA

A LATE PLIOCENE MAMMALIAN FAUNA FROM THE GRANGE BURN, VICTORIA, AUSTRALIA

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TABLE OF CONTENTS

	text	illustration
INTRODUCTION	5	
SYSTEMATIC DESCRIPTIONS		
Metatheria: Marsupialia		
Perameloidea: Peramelidae		
Genus and species indet.	11	88
Phalangeroidea: Phalangeridae: Phalangerinae		
Phalanger cf. *gymnotis*	13	90
Trichosurus sp. indet.	14	90
? *Phalanger, Trichosurus*, or unnamed related genus, sp. indet.	15	90
Incertae sedis: near *Phalanger* or *Trichosurus*	19	
Incertae sedis (minute form)	20	98
Phalangeroidea: Phalangeridae: Burramyinae		
Burramys sp.	22	98
Phalangeroidea: Phascolarctidae: Pseudocheirinae		
Pseudokoala erlita new genus and species	26	100
Pseudocheirus stirtoni new species	34	104
Pseudocheirus marshalli new species	40	116
Pseudocheirus sp.	44	
Phalangeroidea: Macropodidae: Potoroinae		
Genus and sp. indet., near *Aepyprymnus*	45	122
Genus and sp. indet., near *Hypsiprymnodon*	46	122
Sp. indet., with similarity to *Potorous* and *Propleopus*	47	
Dorcopsis sp. indet.	47	124
Phalangeroidea: Macropodidae: Macropodinae		
Thylogale sp. indet.	53	132
Incertae sedis: large-sized forms, two taxa near *Protemnodon*	63	142
Incertae sedis: small-sized forms, near *Dorcopsis and Thylogale*	66	136
Phalangeroidea: Diprotodontidae		
Palorchestes cf. *painei*	66	146
Eutheria: Chiroptera		
Microchiroptera: *Incertae sedis* at all lower taxonomic levels	69	144
Class indeterminate, probably Mammalia		
Incertae sedis at all lower taxonomic levels	70	148
INTERPRETATION OF THE HAMILTON FAUNA	74	
SUMMARY AND GENERAL CONCLUSIONS	79	
ACKNOWLEDGEMENTS	80	
REFERENCES	81	
APPENDIX		
Plates	87	
Graphs	151	

INTRODUCTION

Australian Tertiary mammals were extremely rare prior to the work of Stirton and his colleagues during the last 20 years. The few specimens known previously were noted and reviewed by Gill in a series of papers between 1952 and 1957. In the last of this series he assessed their significance, stratigraphic relationships, and affinities, and he suggested a few other possible Tertiary marsupial localities in Victoria and Tasmania (Gill, 1957).

As a result of the efforts of Stirton's group, this meager knowledge has been added to, and now a tentative outline of Australian mammalian evolution during middle and late Tertiary time is beginning to emerge. Thanks to their concurrent stratigraphic work, the relative geochronologic positions of the various faunae are known (Stirton et al., 1967a, 1968). To date only the New Guinean, Awe fauna, and the Victorian, Hamilton fauna (described here) have been dated isotopically, and thus they will provide a key to late Tertiary faunal correlations in the Australian region as well as give a chronologic correlation with Tertiary faunas in other parts of the world.

Previous work.—The first find of a fossil marsupial from the Tertiary terrestrial deposits of the Grange Burn[1] was the discovery of a single tooth of a potoroine reported by Gill in 1952 and 1953a, and subsequently.[2] It was first identified as that of a cuscus (Gill, 1957 and earlier; Stirton, 1957a). Ride (1964) restudied and re-illustrated the specimen, concluding that it was either a right $M_{\bar{2}}$ or $M_{\bar{3}}$ of a potoroo of nearly the size of *Propleopus oscillans*, but having a morphology closest to *Potorous gilberti*. This tooth was found in the "A" zone of a fossil soil which underlies a basalt flow. Preliminary and progress reports of our work on the fauna from this level appeared subsequently (Turnbull et al., 1965; Lundelius and Turnbull, 1967).

[1] The macropodid jaw from Forsyth's Bank reported by Colliver (1933), Singleton (1935), and Gill (1957 and earlier), and described as a Sthenurine by Stirton (1957) came from shallow water marine beds, stratigraphically beneath the terrestrial deposits. Tedford (1966, p. 57) cast doubt on its unequivocal reference to the Sthenurinae. It does not enter into this report.

[2] Gill 1953 b,c; 1955; 1957; 1965 a,b.

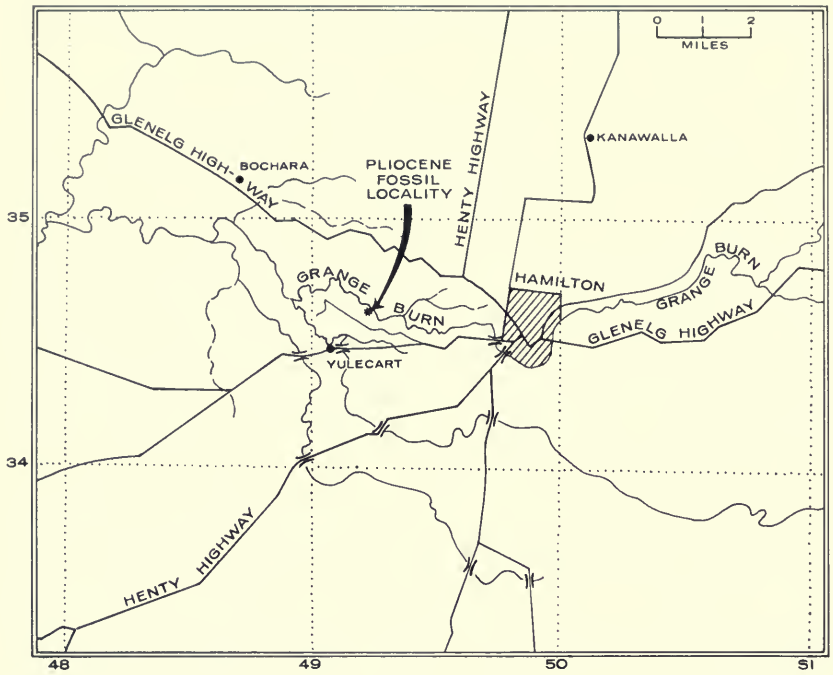

FIG. 1. Map of the Hamilton area in western Victoria showing the location on the Grange Burn of the Pliocene (Hamilton Fauna) fossil locality.

The reported occurrence of Tertiary macropodid remains from fissure fillings in the Bochara limestone of the same area (Glaessner et al., 1960) has been found to be Pleistocene (Glaessner, 1963).

Locality.—The fossils were collected from a deposit at a waterfall on Grange Burn on the George Pelchen property, 4.5 miles west of Hamilton, Victoria (Fig. 1). This is locality no. 10 of Gill (1957).

Stratigraphy and Age.—The stratigraphy of the Tertiary rocks of the Hamilton area has been described by a number of people. Gill (1957) has reviewed the literature, has briefly summarized the Tertiary stratigraphy of the area, and has shown the critical outcrops on his map.

The Tertiary sediments exposed in the natural drainages west of Hamilton consist of marine, shore, and terrestrial deposits. The marine beds are shallow-water limestones, shales, and marls of Miocene (Batesfordian and Balcombian) and Pliocene (Kalimnan) ages. These grade upward into shore facies sands with shell fragment lenses which are overlain by continental sandy fossil soils and lacustrine

clay and sand deposits. These have been considered to be of Pliocene (Kalimnan?) age. The sequence is capped by a basalt.

The following sequence is exposed at the fossil locality on the Grange Burn:

1. Basaltic lava flow. At this outcrop the basalt is vesicular at the bottom, denser in the higher portion. Irregular, vertical structures can be seen which appear to be gas bubble tracks. The lower surface of the basalt is irregular with charred tree stumps projecting into it. The sample for the potassium-argon date reported earlier (Turnbull et al., 1965) was taken five feet above the bottom of the basalt in the denser part. .....6 feet to eroded surface.

2. Tight, non-calcareous silty sand, grey when weathered, blue when fresh. Contains carbonized tree stumps and roots in the living position that show various degrees of charring. The upper two or three inches, which are dark brown to black in color, contain a very large percentage of carbonaceous material. There are many elongate patches of friable, grey to white sand and silt with finely divided carbonized plant material. These are oriented from vertical to horizontal and show branching. They appear to be root channel fillings. The sieve concentrates from which the specimens were picked also contain numerous limonitic and caliche fragments, and basalt chips (which spalled off, or were knocked off from the overlying basalt in procuring the matrix sample). Rarer residues are reddish (contact metamorphosed ?) pieces of clay (seen also on large overturned basalt blocks that had slumped into the streambed), buckshot (goethite magnetite), rounded quartz pebbles, and occasionally fine, hackly, crystalline fragments (some fresh-looking, others weathered) stained with limonite. These contain mainly quartz, feldspar, and mica, and thus appear to be washed in bits of granitic rock. The vast bulk of the sediment is in the clay, silt, and fine sand particle size range.

All the fossils discussed here were collected from this unit which appears to be the "A" zone of a soil. .....1–1.25 feet.

3. Tight, calcareous, grey-green to yellow-green sandy silt containing carbonized plant roots, many of which are oriented vertically and appear to be in the living position. There are also numerous calcareous nodules mainly of two sorts. Most of those in the upper part are about ½ inch in diameter, red to yellow, dense and hard with ferruginous centers. Some of the nodules in the upper part and all in the lower part of this unit are calcareous, have no ferruginous centers, and are less dense than those from the upper part of the unit.

Many of the lower nodules are elongate, oriented vertically, and appear to be cemented root channel fillings. A few deeply weathered marine mollusc shell fragments are recognizable in the lower part. This unit is believed to be the "B" zone of a fossil soil.

. . . . . 3½ feet exposed.

We tentatively accept Gill's soil zone interpretation for units 2 and 3, at least until detailed petrologic analyses of the sediments are available. This soil profile is developed upon and immediately overlies a calcareous near-shore marine sandstone, the Grange Burn coquina, of lower Pliocene (Kalimnan) age (Gill, 1957).

The stratigraphy indicates a post early Pliocene age for the fossils collected from the "A" zone of the soil. This is confirmed by the K/Ar date of 4.35 ± 0.1 m.y. reported by Turnbull et al. (1965). This date is late Pliocene according to the time scale of Evernden et al. (1964). The contemporaneity of the marsupial fauna and the fossil soil with the overlying basalt is indicated by the presence of carbonized tree stumps and roots in the living position in the upper two to three feet of the fossil soil (Fig. 2). Apparently the lava flow cremated a standing forest. It is unlikely that the fossils are appreciably older than the flow because it is doubtful that they would have survived the weathering processes in the soil for any length of time.

Methods.—Matrix was removed from the "A" zone, dried, and wet-sieved in the manner described by Hibbard (1949). All residues above 30-mesh were saved and sorted for bones and teeth. The "B" zone was not sampled because of lack of time and the belief that it was likely to be less productive than the "A" zone. No attempt was made to subdivide the "A" zone. A total of three tons of "A" zone matrix was removed and wet-sieved. This produced approximately 500 pounds of size-graded concentrates which has yielded approximately 150 identifiable teeth or significant tooth fragments[1] representing 18 mammalian taxa.

The material recovered consists almost entirely of isolated teeth and fragments of teeth. Rarely some bone is preserved, mostly in poor condition, but occasionally an unweathered fragment was recovered. No associations were noted in the process of collecting, but some were made later on the basis of the interdental facets. Many teeth were reassembled from fragments and many teeth are unworn.

[1] Subsequently an additional eight tons of A and B zone matrix were taken, but except for seven specimens (PM 16801–PM 16802; NMV–P 26419–P 26420 and P 26422; and PM 16805 and PM 16807) picked from the sieves at the time of processing this sediment, none of this material is available at this time.

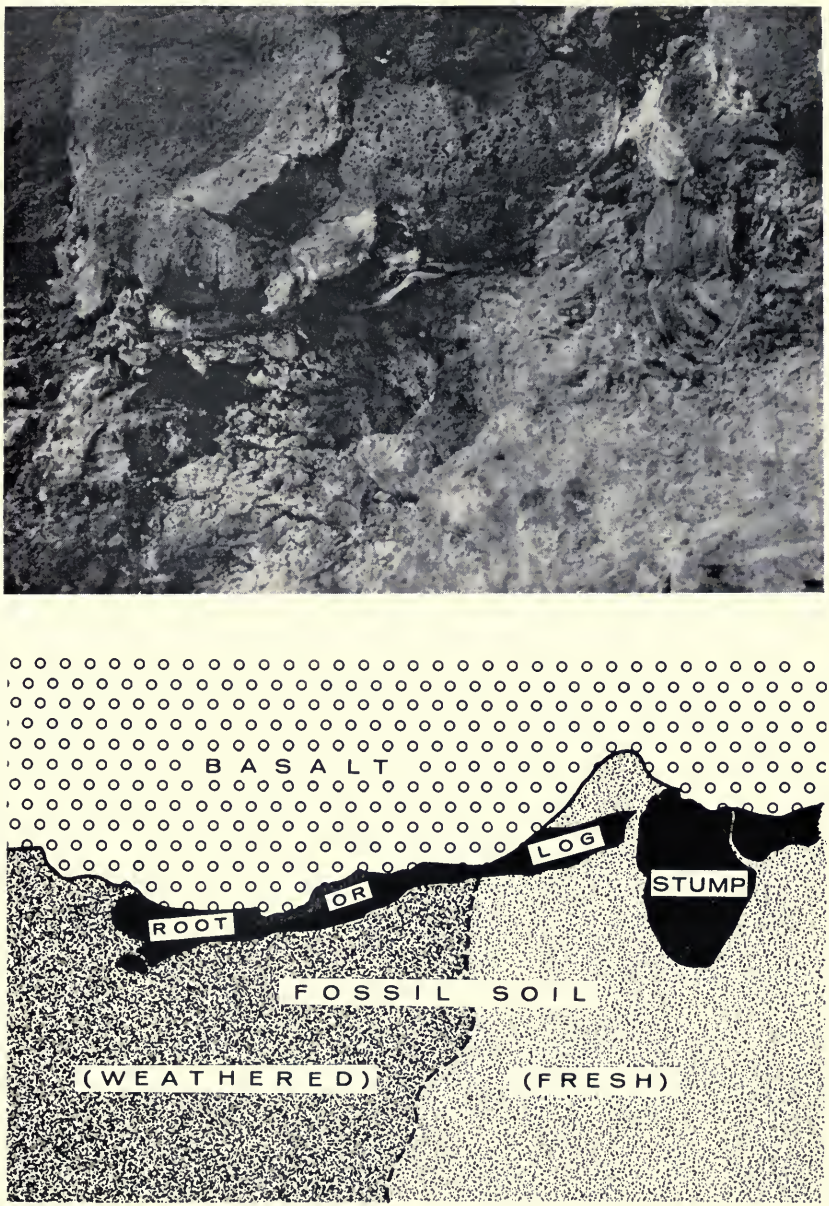

FIG. 2. Close-up view of the contact between the Pliocene fossil soil and the overlying basalt with schematic interpretation. Roots or branches, and the bolus of a tree stump, apparently in the living position, may be seen. Scale is approximately $\times 1/6$.

The teeth exhibit various degrees of weathering which takes the form of solution-pitting on the enamel and often the removal of the roots, the dentine of the crown, or both. Some teeth show no sign of pitting and have the roots well preserved. Others consist only of the solution-pitted enamel caps and the adjacent dentine. This variation in degree of weathering is believed to be a function of the length of time they were subjected to the weathering processes before being sealed off by the lava flow. None of the teeth shows any signs of abrasion such as rounding of the cusps, etc., which would be expected if they had been transported any distance to the site of deposition.

The lack of associations of teeth in jaws has created a problem of designation of types for those species which we believe are represented by more than one tooth. In these cases, a single tooth has been designated the type. The only exceptions are those in which a positive association can be made on the basis of well-defined interdental facets. Where the material is too fragmentary to allow the assignment of a generic or specific name, the fossils are described, figured and compared to Recent and fossil forms.

Abbreviations.—Numbers with the following prefixes denote specimens catalogued in the collections of the institutions indicated.

PM—Fossil Mammal Collection, Field Museum, Chicago.

NMV-P—Paleontological Collection, National Museum of Victoria, Melbourne.

FM—Recent Mammal Collection, Field Museum, Chicago.

UT-M—University of Texas, Vertebrate Paleontology comparative collection of Recent mammals.

AMNH—Recent Mammal Collection, American Museum of Natural History, New York.

UCMP—University of California, Museum of Paleontology.

USNM—Recent Mammal Collection, U. S. National Museum, Washington.

WAM—Western Australian Museum, Perth.

SYSTEMATIC DESCRIPTIONS

Class Mammalia

Infraclass Metatheria

Order Marsupialia

Superfamily Perameloidea

Family Peramelidae

Genus and Species indet.

Material.—The anterior half of a right lower molar, probably $M_{\overline{2}}$ or $M_{\overline{3}}$ (PM 4499); part of a trigonid of a right lower molar (NMV–P 26406); fragment of a left lower molar consisting of the lingual side of the trigonid and anterior cingulum (PM 4446); metaconid fragment of a right lower molar (PM 4600); backside of trigonid of a right lower molar (PM 4748). This material is inadequate for either generic or specific assignment. Plate I, Figures A–F.

Description.—Most of the description and comparison is based on the best specimen (PM 4499); the others conform closely to it except as noted. The following features combine to identify these teeth as belonging to the Permalidae rather than to the Dasyuridae, the only other group with which they might be confused.

1. The anterior cingulum is large and rounded with a shallow but distinct basin. A large anterior cingulum is present in $M_{\overline{2}-\overline{4}}$ of peramelids.[1] This structure is generally much less pronounced in the dasyurids where it is almost straight and is closely appressed to the antero-labial surface of the tooth.

2. The protoconid-paraconid and protoconid-metaconid crests lack the sharp, deep clefts such as are found in the bottoms of the "V"s of these crests in the teeth of dasyurids. In this they agree with the known peramelids.

3. The valley between the paraconid and metaconid is much narrower than in the dasyurids, and is more like that of the peramelids.

[1] The following dasyurids and peramelids were studied: *Sminthopsis* (several species), *Phascogale tapoatafa*, *P. calura*, *Dasycercus blythi*, *Parantechinus apicalis*, *Dasyurus geoffroyi* and *Dasyurus* (*Satanellus*) *hallucatus*, *Sarcophilus harrisi*, *S. laniaris*, *Thylacinus cynocephalus*, *Glaucodon ballaratensis*, *Isoödon*, *Macrotis*, *Perameles*, *Echimypera*, *Peroryctes* and *Ischnodon* ($M_{\overline{2}}$ only, other molars unknown).

4. The hypoconid ridge (Pl. I, A–C, arrow h) of PM 4499 joins talonid and trigonid at the middle of the back of the trigonid. This ridge is somewhat variable in its development and morphology in both peramelids and dasyurids, but the usual pattern is clear for both families. In those peramelids with molars in which this ridge joins the trigonid (i.e., most teeth of most of the living species except $M_{\overline{3}}$ of *Echimypera doreyana*) the junction is usually located either in this region or more lingually. In the small dasyurids this junction is located near the labial side on $M_{\overline{1-3}}$ ($M_{\overline{4}}$s have talonid lingually placed and very reduced in size). In *Isoödon obesulus* the junction of this ridge and the trigonid shows the dasyurid pattern; hence it is an exception.

The anterior cingulum is large and rounded with a shallow basin very much like that of *Echimypera doreyana* (FM-54233). It arises on the antero-labial surface of the protoconid, extends antero-lingually, and meets the paraconid near its base by turning abruptly posteriorly at the antero-internal corner of the tooth. A tiny cuspule is located on the cingulum just anterior to the paraconid. The cingulum does not approach the apex of the paraconid, as in *Isoödon*, but remains well below it, as in *Echimypera*, *Perameles*, and *Peroryctes*. The antero-lingual end of the cingulum is in line with the paraconid and metaconid. This condition is found in *Peroryctes longicaudata* and in $M_{\overline{1-2}}$ of *Peroryctes broadbenti* and is approached in *Perameles gunnii* and *Echimypera doreyana*.

The paraconid and metaconid of the Hamilton peramelids are relatively farther apart than in living peramelids, except *Peroryctes*. The protoconid is the largest cusp. It is followed in descending order by the metaconid and paraconid, as in most other peramelids except *Macrotis lagotis* (which has an enlarged metaconid) and *Choeropus* (in which the paraconid and metaconid are equal in size and are very close together). The tooth is less hypsodont than are any of those of living peramelids except *Peroryctes*. There is only the beginning of cusp hypsodonty (see White, 1959), such as is seen in *Perameles*.

The postero-lingual border of the metaconid has a ridge running from the apex to the base. The lower molars of *Peroryctes longicaudata*, *P. broadbenti*, and *Echimypera doreyana* have a similar ridge which joins the ridge that runs to the entoconid. The ridge on the metaconid is absent in other peramelids. The posterior border of the trigonid of PM 4499 is slightly concave (more so than in *Peroryctes longicaudata* and $M_{\overline{1-2}}$ of *Echimypera doreyana*).

There is a saddle-shaped connection between the remnants of the hypoconid ridge and the metaconid-entoconid ridge in PM 4499. This implies the existence of a basined talonid. In NMV-P26406 the break at the back of the trigonid suggests that the talonid basin, if present, did not extend forward to meet the trigonid for there is no indication of a hypoconid ridge (see Pl. I, Fig. F). Instead, the surface is convex and slopes rapidly labially. It is characteristic of the $M_{\frac{4}{4}}$s of most peramelids that they lack a talonid basin. There is usually a ridge connecting the metaconid and entoconid. The position of NMV-P26406 within the molar series is uncertain: it is most likely an $M_{\frac{4}{4}}$ but possibly it is an $M_{\frac{3}{3}}$ similar to that of *Echimypera doreyana* (because of the great width of the talonid indicated by the break surface).

Measurements.—

PM 4499

Length of trigonid (paraconid-metaconid length).....1.49 mm.
Length of trigonid plus anterior cingulum.....1.95
Maximum width of trigonid (parallel to its back edge)...1.87

NMV-P 26406

Maximum width of trigonid (parallel to its back edge)...1.83

Discussion.—It is impossible to assign these Hamilton specimens to a genus or species or even to be sure that they belong to the same genus or species. They resemble both *Peroryctes* and *Echimypera* more than any other peramelid in the spacing of the trigonid cusps, kind and degree of hypsodonty, and a large-basined anterior cingulum. The Hamilton specimens show roughly the same degree of divergence from the basic dasyurid lower molar pattern as do *Peroryctes* and *Echimypera*

Superfamily Phalangeroidea
Family Phalangeridae
Subfamily Phalangerinae
Phalanger Storr, 1780

Phalanger cf. **gymnotis**

Material.—Nearly complete crown of left $P_{\frac{4}{4}}$ or right $P^{\frac{4}{4}}$ (PM 4457, Pl. II, Fig. C).

Description.—The tooth is a high, narrow, flat-sided blade with a rounded crest and at least four transverse ridges. In crown view the

antero-labial surface is convex and set off by ridges. The anterior ridge extends from the axial crest antero-lingually toward the base of the crown. The ridge separating the antero-labial surface from the labial surface extends in a weakly sinusoidal curve to the base of the crown. This ridge is continuous with a similar ridge on the lingual side of the tooth. The other three ridges do not extend more than 25 per cent of the distance to the base of the crown. They are approximately equally spaced and have distinctive, bluntly pointed apices. The middle two cross ridges are the same size and are slightly larger than the anterior and posterior ridges. All transverse ridges retain their identity where they are folded over the axial crest, rather than blending into it, as is the case in *Phalanger orientalis* and *P. maculatus* and in both species of *Trichosurus*. The axial crest of the tooth reaches the same level between the four transverse ridges. Behind the posterior ridge it descends sharply to a broken surface so as to make it appear probable that the greater part of the crown is preserved. The best comparison is with the fourth premolars of *Phalanger gymnotis* (FM 31861) which show no major differences from this fossil.

Discussion.—See p. 20.

Trichosurus Lesson, 1828

Trichosurus sp. indet.

Materials.—Left I^3 (PM 4563, Pl. III, Figs. D and E); two partial premolars, either upper right or lower left preserving the anterior one-third of the tooth (PM 4556 and PM 4557, Pl. II, Figs. D and B, respectively).

Descriptions.—The I^3 is represented by one unworn tooth (PM 4563). The occlusal surface consists of a sharp edge which extends straight to the posterior corner, then upward along the posterior side, and gradually loses its sharp-edged character. At its anterior end this sharp edge merges with ridges which extend short distances above the occlusal surface on the outside and inside of the tooth. The outside one is stronger. The labial anterior ridge extends upward and posteriorly, and joins one extending upward from a cuspule located at about the midpoint of the occlusal surface. These two ridges form a shallow triangular-shaped basin on the labial side of the tooth. In the Recent *Trichosurus vulpecula* wear rapidly eliminates this basin. The posterior part of the labial side of the tooth is almost flat with only a trace of the sulcus seen in the Recent species.

The blade-like occlusal surface is turned lingually. The anterior surface of the tooth is broad and gently concave. The central cuspule on the occlusal surface also gives off a low ridge on the lingual surface. This ridge extends anteriorly and upward and disappears. There is little or no sign of such a ridge in the Recent form. The fossil tooth is the same size as its counterpart in the Recent species of *Trichosurus* and is markedly larger than the reduced I^3 of *Phalanger*.

The two premolar fragments differ only slightly from one another. They are at the lower end of the size range for modern *T. vulpecula*. Both have the typical three anterior ridges which extend toward the tooth base as in *T. vulpecula*, the central ridge being the largest and extending nearly in the axial plane. This ridge lacks the sharpness of its counterpart in the Recent form. The labial ridge extends from the apex of the crown to the base in a nearly straight line, rather than being markedly curved in a posterior direction. The lingual ridge is more pronounced in the fossil than in the Recent species of *Trichosurus* and it is better developed at the apex in PM 4557 than in PM 4556. It extends to the tooth base in a straight line in the former. In PM 4556 this ridge curves posteriorly at the base of the crown. The antero-labial surface in both teeth is convex except for a slight depression near the apex. The antero-lingual surface is slightly narrower than the antero-labial surface and is weakly concave in PM 4556. In PM 4557 it is concave at the apex, but flat at the base. These teeth are markedly different from the premolars of *Phalanger orientalis* in which the antero-lingual ridge is virtually absent.

Discussion.—See p. 20.

? **Phalanger** or **Trichosurus** or an unnamed, related genus

Sp. indet.

The collection contains five specimens that appear to represent the same species. These teeth share certain features typical of various species of *Phalanger*, and other features of species of *Trichosurus*. We are convinced that they represent a new species, but cannot make a generic assignment because of inadequate material. This species may belong to either of the above-named genera, or to an as yet unnamed intermediate genus.

Materials.—A right M^1 (PM 4571, Pl. IV); a left upper molar fragment (PM 4728); a molar fragment, probably part of a right upper, with part of posterior cingulum, hypocone, metacone, and the

metaloph preserved (PM 4735); a right M_1 (PM 4555, Pl. III, Figs. A–C); and a right M_3 (NMV–P 26407, Pl. V).

Descriptions.—The M^1 (PM 4571) is very similar to that of *Trichosurus vulpecula* and *T. caninus* (USNM 221121) but differs in having a well-developed parastyle which is well separated from the paracone (Pl. IV). This cusp (parastyle) is variable in modern *T. vulpecula* but does not attain the size or distinctness seen in the fossil specimen. The condition is approached quite closely, however, in a Western Australian specimen, *T. vulpecula* (UT-M-850), in a juvenile from Victoria (FM-98897), and in a specimen of *Phalanger orientalis* (FM-54021), all of which have a good parastyle. A small cingular cuspule (mesostyle?) is present on the labial side between the metacone and paracone. This cuspule is variable in the Recent *T. vulpecula* but is quite like that of the fossil in UT-M-850. The ridges which connect protocone and hypocone form a V-shaped junction in the fossil, a U-shaped one in Recent *T. vulpecula* from Western Australia, and a U-shaped, but narrower one in the living eastern form. In size the tooth falls at the low end of the range when compared with 23 specimens from widely separated localities in Australia (from Northeast Cape, the Southwest and Nullarbor Plain in Western Australia; and from South Australia, Victoria, Tasmania, and Northern Queensland). The M^1 is narrower (absolutely and relatively) than in any of the specimens available for comparison. The unworn enamel surfaces are more irregular than in the Recent species but are not crinkled as in *Phalanger*.

A left upper molar, probably an M^2 (or M^3), is represented by a slightly worn paracone (PM 4728). It is a nearly square fragment, with its most pronounced feature being the anterior cross-loph (protoloph). This loph runs horizontally almost straight across the fragment, when viewed occlusally in normal orientation. The anterior edge of the procingulum is broken away, but the valley behind the cingulum is well delimited. The sloping anterior and posterior faces of the protoloph are nearly equal, weakly crenulated, and are oriented at 90° to one another, each at 45° to the occlusal plane. The labial side of the cusp meets the gently saddled protoloph at the apex of the paracone at an angle of about 90°. It is a flat, gently sloping, plane surface. Crests run forward and backward from the apex of the paracone at the junction of this surface with the inclined faces of the protoloph. The anterior of these crests leads to the anterior cingulum. The posterior leads down toward the transverse valley

where it bends sharply lingually just in front of the deepest part of the valley. A trace of a parastyle is present on the forward crest near the antero-labial corner of the tooth. Wear marks the crest of the protoloph, a distinct anterior facet, and a broad region of the posterior-facing surface of the protoloph. The fragment resembles *Phalanger* teeth in the subequal proportions of the anterior and posterior faces of the protoloph, but is more like *Trichosurus* teeth in the form and character of its enamel surface sculpture.

The right metaloph (PM 4735) has the enamel surface pitted to a greater extent than in *T. vulpecula* but not so deeply as in *Phalanger maculatus* or *P. orientalis*. The metaloph ridge resembles the protoloph of PM 4728. The anterior face of the metaloph is slightly larger than the posterior one. The difference is less than that seen in upper molars of *T. vulpecula* but more than in either *P. orientalis* or *P. maculatus*.

The M_T (PM 4555), a right, differs from that of most *T. vulpecula* in a number of ways, from *T. caninus* in other ways, and from *Phalanger* in still other ways, but at the same time shows many similarities to each of these. The tooth is both laterally compressed and tapered in its anterior half, but is broad and square in outline posteriorly (Pl. III, A–C). The lingual side of the anterior part of the tooth is strongly concave between the anterior ridge of the protoconid and the metaconid. In the middle of the concavity is a small pillar-like, rounded crenulation. It starts near the base and fades out upward. This is absent in the Recent species of *Trichosurus,* but a similar or more pronounced ridge is preserved in *Phalanger orientalis* and *P. maculatus*. The protoconid and metaconid are distinct and subequal, but are close together as in *Phalanger*. They are at the same height and are joined by a short ridge which has no depression along it. These cusps are more widely separated in all specimens of *Trichosurus* available for comparison. *T. vulpecula* has metaconid relatively smaller than protoconid. The labial side of the protoconid slopes steeply as does the hypoconid with no sign of a cingular bulge as in *T. vulpecula*. (The base is broken and its absence may be due to this.) A ridge extends downward and posteriorly from the metaconid to the transverse valley, and disappears as it turns toward the center of the tooth. It does not join the anterior ridge from the entoconid. A U-shaped notch is formed as in NMV-P 26407. Also, as in NMV-P 26407, the ridges joining protoconid and hypoconid meet to form a "V" rather than a flat-bottomed "U." The posterior crest of the protoconid is slightly convex labially and the anterior crest of the

hypoconid is straight. In the Recent *Trichosurus vulpecula* the posterior crest of the protoconid is concave labially and the anterior crest of the hypoconid is either curved or sharply angled. This difference results in a relatively wider central basin in the Hamilton fossil. The metaloph is broad and continuous, though it is depressed in the middle. The slightly worn enamel is ornamented with irregular rounded pits and ridges as in NMV-P 26407. Very small wear facets appear on some of the crenulations and also on the center of posterior cingulum.

The $M_{\bar{3}}$ (NMV-P 26407, Pl. V) shows no significant difference in proportions from the Recent *Trichosurus vulpecula.* The posterior and anterior ridges from metaconid and entoconid are well defined as in the eastern Recent form and differ from the Western Australian form in which these ridges are much reduced. The posterior ridge of the metaconid and the anterior ridge of the entoconid do not meet but turn toward the center of the tooth leaving a U-shaped channelway that becomes rapidly V-shaped as it extends laterally into the central basin of the tooth. This character is variable in the Recent form. It does not appear on any of the University of Texas specimens, but wear makes interpretation difficult in most of them. There is no corresponding open channel between the protoconid and hypoconid. Instead, the posterior ridge of the protoconid extends diagonally straight toward the entoconid and is joined in the transverse valley by a recurved ridge that runs forward from the hypoconid. These ridges form a V-shaped junction in the fossil, and a flat-bottomed U-shaped junction in the Recent *T. vulpecula.* The crosslophs are continuous and not broken by clefts. The profiles of the crests are more or less U-shaped although the anterior one is (weakly) V-shaped. These features are variable in the Recent form. A low but distinct cusp is located on the labial side of the anterior cingulum. It is only tenuously joined to the protoconid by the outer part of the cingulum where this structure crosses the valley between the two cusps. In the posterior molars of most specimens of the Recent species the cingular cusp is also joined to the protoconid by a broad, low ridge which divides the anterior cingular basin into two, a larger inner one and small but deep outer one. A posterior cingulum is present which forms a deep, transversely elongated posterior cingular basin. The posterior cingulum of *Trichosurus* $M_{\bar{3}}$s is highly variable. In some it is pronounced and delimits a well-defined basin, in others it is incomplete lingually so that the basin opens behind the entoconid, and in others it is both incomplete and much shortened. In *Phalanger*

the posterior cingular basin tends to be open and broad. It is relatively shallow and the cingulum is low. The antero-labial corner of the tooth has a very shallow indentation. In *Phalanger* and most specimens of *Trichosurus vulpecula* this is a small but definite pit formed by the backward and downward extension of the anterior cingulum. The unworn enamel surfaces are more uneven but do not approach the condition in *Phalanger*.

Measurements.—

PM 4571, a right M^1	Length	5.16 mm.
	Anterior width	3.49
	Posterior width	3.49
PM 4555, a right M_1	Length (slightly broken)	5.80
	Anterior width	(too broken to measure)
	Posterior width	3.70
NMV-P 26407, a right M_3	Length	5.07
	Anterior width	3.68
	Posterior width	3.71

Discussion.—See p. 20.

Incertae sedis: near *Phalanger* or *Trichosurus*

Sp. indet.

In addition to the teeth of large phalangerines described above, there are five tooth fragments that we can only tentatively and dubiously place in this grouping. They are PM 4721, PM 4722, PM 4723, PM 4724, and PM 4726. Of these only PM 4722 is illustrated (Pl. II, Fig. A). It appears to be the end of the left? upper canine. It very closely resembles the end of the canine of Recent *Trichosurus vulpecula* from eastern Australia (FM 60935). The cross-section is roughly that of a diamond, with the long axis antero-posterior. The posterior ridge of the Recent form has a small to minute subsidiary cuspule. In the fossil this cuspule is minute and is very closely appressed to the main cusp. It differs from *Phalanger* which has conical recurved canines. It differs from the potoroines (*Bettongia, Potorous, Hypsiprymnodon*) which have the upper canine strongly compressed laterally. The broken posterior surface leaves interpretation of this fragment as a canine in some doubt. It shows an inverted "V" shape that can be variously interpreted as a diagonal break along the back of the canine, or as a vertical break running transversely across a small blade-like tooth.

Discussion of the large phalangerines.—There seems to be no doubt that at least two taxa are represented by the materials described on pages 13 to 19. It also seems certain on the basis of the $P\frac{4}{4}$s that both *Phalanger* and *Trichosurus* are represented. The $P\frac{4}{4}$s of *P. gymnotis* are very distinctive, and the close resemblance of the Hamilton specimen to them leaves little doubt as to its relationship. The *Trichosurus*-like $P\frac{4}{4}$s are evidence that this genus is represented, but probably by a species different from any presently known. This is supported by the $I^{\frac{3}{3}}$ which is virtually identical to that of the living *T. vulpecula.*

The molars all share various morphologic features of the genera *Phalanger* and *Trichosurus.* In the case of the V-shaped junction of protocone-hypocone ridges and protoconid-hypoconid ridges (as well as the near proximity of protoconid and metaconid in M_T) they are closest to *Phalanger.* Regarding features such as depth of posterior cingular valley and height of the posterior cingulum, they appear to be closest to some specimens of *Trichosurus.* In the case of the degree of pitting and crenulation of the enamel surface, they are quite intermediate between the two genera. *Wyulda squamicaudata* (WAM-B1920) was also compared, and it agrees with *Trichosurus* in this regard. Both *Trichosurus* and *Phalanger* have species that show tendencies to bridge the gap.

Therefore, in dealing with the large phalangerine teeth, we have no way of telling with certainty which of the front teeth (if any) go with the molars. There are differences between the fossil Hamilton molars and those of our comparative materials of *P. gymnotis* (FM 31861), while the $P\frac{4}{4}$s correspond very closely to those of the modern species. The differences between the Hamilton molars and a broad suite of *T. vulpecula* is, if anything, even greater, so that their possible correlation with the preserved anterior teeth assigned to *Trichosurus* sp. indet., seems even less likely. Hence we know that the fauna certainly contains two, and may contain three related, large phalangerines.

Incertae sedis (minute form)

Genus and sp. indet.

Material and Description.—A minute phalangerine approximately the size of *Acrobates, Distoechoerus,* or *Cercartetus,* is represented in the Hamilton fauna by two left lower incisors NMV-P26408 and PM 4553 (Pl. VI, Fig. B) which are very similar to one another in

almost every detail. We cannot assign them positively to any genus but comparisons with these three are closer than with other genera of minute-to-small phalangerines.

The fossils have a flatter, less arched, and more spatulate upper surface than do the $I_{\bar{1}}$s of *Petaurus* (FM 56318) which are also much longer. There is not as well defined an outer ridge as in *Petaurus*.

The fossil $I_{\bar{1}}$s are more like those of *Cercartetus concinnus* (FM 34721 and UT-M 831, 832, and 842) or *Acrobates pygmaeus* (FM 69898) especially as to size. They have a better defined internal ridge than does *C. concinnus*, and are more curved and more evenly curved longitudinally in the flattened plane than in *C. concinnus*. The medial surface shows a trace of a shallow longitudinal trough (more pronounced in NMV-P26408 than in PM 4553), which apparently is readily erased by interdental wear. A similar situation exists for *C. concinnus*. The fossil teeth have a lateral longitudinal ridge as in *C. concinnus*, but it is set off from the bulk of the tooth by a narrow groove. The tips of the fossil teeth are more rounded and are less symmetrical than in *C. concinnus*.

The Hamilton specimens are slightly less curved and are less tapered when viewed from above (in the horizontal plane) than are the *Acrobates pygmaeus* specimens available for comparison (FM 60898 and Monash University no. 974). *A. pygmaeus* has a better developed external ridge than does either of the fossils or *C. concinnus*. In *A. pygmaeus* near the back edge of the crown, this ridge swings across the dorsal surface of the tooth and becomes continuous with an equally developed internal ridge. In *C. concinnus* the comparable ridges die out posteriorly. The posterior ends of the Hamilton specimens are broken, and the course of the ridges cannot be determined.

In comparison with *Distoechoerus pennatus* (AMNH-104058) in which the dorsal surface of the $I_{\bar{1}}$ is convex, the fossil teeth are flatter, and they are also less pointed.

They differ from *Burramys* in:

1. Cross-section.—*Burramys* has a very deep oval section with the long axis of the oval vertical. The Hamilton teeth are more flattened, and the long axis of the oval is more nearly horizontal.

2. Ridge development.—The Buchan *Burramys* available to us has none, but the tip of the tooth is broken, and *B. parvus* from Wombeyan Cave has them strongly developed, but only distally

on the tooth. The Hamilton fossils are ridged for most of the length of the crown.

3. Torsion.—The Hamilton teeth show torsion, *Burramys* $I_{\frac{1}{1}}$s do not.

In comparison with *Tarsipes spenceri*, the fossils differ markedly in curvature and taper, *T. spenceri* being straight, with a very gentle taper and with much less torsion. Also, quite unlike the Hamilton teeth, the crown in the $I_{\frac{1}{1}}$s is expanded over the root in *T. spenceri* especially on the dorsal surface (UT-M8294 and FM 34719).

Although the closest resemblance is to the $I_{\frac{1}{1}}$s of *Cercartetus concinnus* and *Acrobates pygmaeus*, there are enough differences from both to preclude assignment of the fossils to either, and to suggest that they probably represent an unknown taxon.

Subfamily Burramyinae

Burramys Broom, 1895

Burramys sp.

Material.—Left $P_{\frac{3}{3}}$, posterior three-fourths of tooth (NMV-P26409, Pl. VI, Fig. C); right $P_{\frac{3}{3}}$, anterior third of tooth (PM 4439, Pl. VI, Fig. D); right $P^{\frac{4}{4}}$, antero-internal corner of tooth (PM 4459, Pl. VI, Fig. F); and left $M^{\frac{2}{2}}$, a complete enamel cap (PM 4470, Pl. VI, Fig. E). This material is inadequate to serve as the basis for designating a new species of *Burramys*, yet we believe that it represents a new form differing slightly from *Burramys parvus* from the Wombeyan Caves and from the Buchan *Burramys*.

Description.—The $P_{\frac{3}{3}}$ is a high, laterally compressed, serrate, blade-like tooth. There are six grooves preserved on each side of the most complete specimen (NMV-P26409). The anterior end of this specimen is broken away and it is not possible to be sure of the total number of grooves in the intact tooth. However, the crest of the tooth begins to curve downward at the break, and it is doubtful that there were more than six or seven grooves on the tooth. The $P_{\frac{3}{3}}$ of the Buchan specimen has six well-defined grooves plus a minute one in front of these on the lingual surface, seven on the labial. In the unworn $P_{\frac{3}{3}}$ of *Burramys parvus* from Wombeyan (PM 5936) there are seven distinct grooves on both sides, plus a minute antero-lingual one.[1] In a worn Wombeyan specimen (PM 16185) five

[1] Best seen at a magnification of about × 50. This feature also is present on PM 16185.

grooves and a trace of a sixth appear on the labial side, and six with a trace of a seventh may be seen on the lingual side.

The antero-internal edge of the $P_{\frac{3}{4}}$ of the Hamilton *Burramys* (PM 4439, Pl. VI, Fig. D) has a ridge that is contiguous with the axial crest of the tooth. This ridge, here termed the antero-axial ridge, turns lingually, then somewhat posteriorly, as it descends in a smooth curve to the base of the tooth. It forms a curb which sharply delimits the convex anterior face from the ridged and grooved lingual side of the tooth. The antero-external margin has no such sharply defined line of demarcation separating anterior face from the slightly convex labial side with its ridges and grooves. There the anterior three or four sets of ridges and grooves fade out and merge with the bulging anterior face which is progressively swept back ventrally. The first ridge trails off at approximately one-third of the distance from crest to base of tooth. The subsequent ones are progressively longer. In the Buchan and Wombeyan specimens available for comparison, the first ridge extends approximately one-half and two-thirds this distance, respectively, before disappearing. The anterior surface is more developed and more bulbous in the Hamilton form than in the others.

The grooves on the lingual side of the tooth are slightly closer together toward the tooth base than those on the labial side. This is unlike both the Wombeyan and Buchan specimens in which the spacing of the grooves is the same on both sides. The first three grooves on the lingual side merge toward the root to form a single broad open groove. The second ridge extends farther toward the root than the first. In the Buchan and Wombeyan specimens, only the first two of the lingual grooves merge, and the first ridge extends farther toward the root than in the Hamilton specimen.

The cutting edge of the tooth (best seen in NMV-P26409) is straight with small cusps marking the junction of the ridges on either side of the tooth. The posterior end has a laterally compressed cusp which is two or three times the size of the more anterior cusps. In these two characters it differs from both the Buchan and Wombeyan forms in which the $P_{\frac{3}{4}}$s have a crest that is arched and in which the posterior cusp is relatively smaller.

The postero-lingual surface of the tooth has two very faint ridges which are only one-half the length of the others (not included in ridge count given above). They converge toward the crown, but do not meet. The anterior ridge of the pair is parallel to the more

anterior ridges. There seem to be no comparable ridges on the $P_{\frac{4}{4}}$s of the Wombeyan and Buchan specimens.

There are wear facets at the top of the outside of the last three ridges and the larger posterior cusp. The posterior end is concave. This concavity is bordered lingually by a ridge which extends down the posterior side of the tooth from the large posterior cusp.

The $P^{\frac{4}{4}}$ is represented by a very small fragment, with a portion of the anterior edge and lingual side of the tooth (PM 4459, Pl. VI, Fig. F). The anterior edge has the same smooth convex surface and sharp, limiting antero-axial ridge as the $P_{\frac{4}{4}}$. The antero-axial ridge is less pronounced than in the $P_{\frac{4}{4}}$. In addition to the antero-axial ridge, five ridges and six grooves are present on the lingual side. The first two ridges merge with the antero-axial ridge, the first very close to the broken edge near the crest and apparently well above the root. The second extends farther toward the root before it merges with the anterior ridge. The third and fourth ridges disappear near the base of the tooth without joining either the anterior ridge or one another.

In the specimens from Buchan and Wombeyan, the first ridge runs parallel and very close to the (weakly developed) antero-axial ridge for about one-half to two-thirds of its length before joining it. The second ridge is parallel to the first and disappears closer to the roots without joining any other ridge.

The left $M^{\frac{2}{2}}$ of the Hamilton *Burramys* is known from a single, very low crowned tooth (PM 4470, Pl. VI, Fig. E). The tooth consists of an unworn enamel cap. It is not quite square in outline, the posterior width is less than the anterior width. Cusp size order is as follows: protocone > paracone $\cong$ hypocone > metacone. Rounded ridges extend both anteriorly and posteriorly from paracone and metacone. The anterior one from the metacone and the posterior one from the paracone do not join, but end close together with a valley between them. Protocone and hypocone are blunt and more rounded than the other cusps. A low, rounded ridge extends from protocone toward paracone, but does not quite join the corresponding ridge from the paracone. A very narrow, tiny but distinct, groove located about in the axis of the tooth separates them. A continuous low broad ridge connects the metacone and hypocone. The region between the two transverse ridges is flat. There are anterior and posterior cingulae. The anterior one has a straight anterior border and is flat bottomed, not basined. The posterior cingulum is bulged posteriorly and is slightly basined. The anterior cingulum joins the

anterior crest of the paracone and forms a slightly differentiated cuspule (? "parastyle").

The Hamilton molar is quite similar to M^2 of *Burramys* from Buchan and Wombeyan Caves, but differs in the following ways:

1. slightly smaller than the Buchan form (Wombeyan and Grange Burn forms about equal, see measurements),
2. absence of an external stylar cusp (cusp "b" of Bensley, 1903 and "B" of Simpson, 1929),
3. more rounded posterior margin,
4. relatively wider anterior cingulum,
5. lower crowned with lower cusps and ridges, and
6. less basined, more open central portion of tooth.

It shows some similarity to M^3 of *Petaurus breviceps* (FM 60939) but differs in the following ways:

1. anterior cingulum relatively wider,
2. transverse ridges show less slope toward center of tooth,
3. lower crowned and less sharply crested,
4. apparent absence of a lingual, ridged bulge on the protocone, such as is characteristic of *Petaurus*,
5. central part of tooth a broad, flat-bottomed transverse valley rather than a basin, and
6. anterior transverse ridge is broken by a small cleft.

Measurements.—See Table 1.

TABLE 1.—Comparison of M^2s of various specimens of *Burramys* (in millimeters)

	PM 4470 Hamilton	Wakefield Buchan Cave	PM 5934 Wombeyan Cave *Burramys parvus*
Length M^2	1.2	1.3	1.2
Anterior width	1.2	1.4	1.3
Posterior width	1.0	1.2	1.1

Discussion.—The Hamilton specimens have characters which indicate that they represent a species of *Burramys* distinct from *B. parvus* from the Wombeyan Caves and the form from the Buchan Caves. Several of these characters, such as the large posterior cusp on P_4, straight crest of P^4, low crown of M^2, and absence of a distinct antero-external stylar cusp on M^2, indicate that the Grange Burn form is more primitive than the other two. Consistent with this interpretation is its greater antiquity (Pliocene *vs.* Pleistocene age for both

the Buchan and Wombeyan forms). The characteristic anterior edges of $P\frac{4}{4}$ may also represent a more primitive stage of blade development or, perhaps equally probable, a different specialization.

Family Phascolarctidae

Subfamily Pseudocheirinae

Pseudokoala[1] new genus

Diagnosis.—The same as for the species *P. erlita* until other species are discovered and a broadened diagnosis is required.

Pseudokoala erlita[2] new species

Holotype.—Two separated teeth, L. M^{3-4} (NMV-P26399, Pl. VII, Figs. A–E and NMV-P26400, Pl. VIII, Fig. A; Pl. VII, Figs. C, E) which are shown by the interdental facets to have been adjacent teeth, constitute the type.

Referred specimens.—A single L. M_1 (PM 4588, Pl. VIII, Fig. B).

Diagnosis.—An animal with M_1 and M^{3-4}, large (see *Measurements*), almost as long but narrower than in *Phascolarctos cinereus*, and very low crowned. Paracone and metacone of M^3 elongate antero-posteriorly as in *Pseudocheirus*. Internal ridges of these cusps smaller and weaker in their development than the ectoloph ridges, as in *Pseudocheirus*. Ectoloph stands nearly vertical, quite unlike that of phascolarctines and in contrast to all other pseudocheirines except the new and yet undescribed Kutjamarpu form.[3] Ectoloph ridge forms a "W"-shape, whose angles in both crown and side view are 120° or greater; this is in contrast to other known phascolarctids which have angles approximating 90° or less. Associated with the ectoloph there is a small transverse ridge (modified ornamentation) in the mesostylar region, as in the known phascolarctines. Mesostyle well developed unlike that of phascolarctines, and like that of pseudocheirines. Protocone and hypocone low, blunt, and weakly crescentic with broad and flat, nearly horizontal labial faces. This

[1] In allusion to the size and similar superficial appearance of these teeth to those of the koala.

[2] The species name is a South Australian aboriginal word meaning ancient.

[3] A cast of this pseudocheirine (UCMP 71664) generously provided by M. O. Woodburne. Its ectoloph stands nearly as vertical as that of M^3 of *Pseudokoala erlita*.

combination of features is unique. $M_{\overline{1}}$ with trigonid more like that in pseudocheirines than that in *Phascolarctos cinereus*, i.e., paraconid is developed and distinct, and protoconid is connected by a sharp crest to the paraconid-metaconid crest near the front of the metaconid somewhat as in *Pseudocheirus* (*Pseudocheirops*) *archeri*. $M_{\overline{1}}$ like that of *Perikoala palankarinnica* in having a well-developed paraconid, but differs in that it has a distinct metalophid which is lacking in *P. palankarinnica*. Ornamentation is coarse, rounded, anastomosing, and virtually confined to the central basin in $M^{\underline{3}\ \underline{4}}$, and is more extensive in $M^{\underline{4}}$ than $M^{\underline{3}}$ or $M_{\overline{1}}$.

NMV-P26399-L $M^{\underline{3}}$, Pl. VII, Figs. A–E

This tooth is more elongate than its homologue (or $M^{\underline{1}}$ or $M^{\underline{2}}$) in *Phascolarctos*, or the $M^{\underline{2}}$ of *Perikoala* or the $M^{\underline{1}}$ of *Litokoala* (Stirton, Tedford and Woodburne, 1967). The hypocone is blunt, with a gently rounded internal face, and is not strongly crescentic as in most *Pseudocheirus*. Apparently the protocone had a similar form. Ridges which give crescentic form are present but are weak, broad, and low. This is different from all living species of *Pseudocheirus*. The posterior ridge of the hypocone is obliquely beveled by a wear facet. It runs directly to the posterior edge of the tooth in a gentle, labially-curved arc, then turns sharply labiad and joins the ectoloph at its base near the postero-labial corner of the tooth to form a shallow, closed posterior basin. The antero-internal corner of the tooth (including much of the protocone) is missing so the presence of similar ridge and basin in this region is uncertain but is suggested by what is preserved. The anterior ridge of the hypocone extends in a slightly meandering path to the postero-internal corner of the base of the paracone. There it joins a ridge on the paracone by means of a minute spur that crosses the intervening cleft. The paracone and metacone are low but pointed and the ectoloph ridges are worn slightly: the enamel has been breached only at tips of cusps. Each has a low, rounded ridge on the antero- and postero-internal faces. The anterior one of the paracone extends from the apex of the cusp to the base but does not join the anterior edge of the tooth. The posterior one of the paracone extends from the apex to near the base where it divides. One branch of this division continues in line, to meet the aforementioned ridge and spur from the hypocone, while the other swings medially at the posterior end of the protoconule. The anterior one of the metacone is irregular, gives branches, and

joins the metaconule. The posterior one of the metacone joins the posterior end of the metaconule. Most of these internal ridges of paracone and metacone are found in *Pseudocheirus archeri, P. lemuroides, P. herbertensis* (posterior one on paracone only), and *Schoinobates volans.* They are best developed in the former species and grade roughly to the latter. They are absent or only incipient in *P. peregrinus* and *P. occidentalis.* They are well developed in *Phascolarctos cinereus* and *Litokoala kutjamarpensis.* In all living species of *Pseudocheirus, Schoinobates,* and *Phascolarctos* the ridges on the paracone and metacone are nearly straight, although in *Pseudocheirus archeri* (and occasionally in the others, especially in the anterior molars) they divide near the base of the cusp to contribute to the complex enamel ridging characteristic of that species. In *Phascolarctos cinereus* the posterior ridge of the paracone is the best developed of the four.

The parastyle and mesostyle are low and rounded, much as in *Pseudocheirus peregrinus* but relatively smaller. The mesostyle is not bifurcate as in *P. peregrinus, P. archeri,* and *Schoinobates volans.* The parastyle and mesostyle do not have the blade-like wings which in *P. archeri* extend posterior from the parastyle and both anterior and posterior from the mesostyle. No external cingulum is present such as in *P. herbertensis.* The central part of the outside surface of both the paracone and metacone has a gently convex central ridge as in *Pseudocheirus peregrinus, P. herbertensis, P. occidentalis,* and *P. convolutor. P. archeri* has a well-defined though broad ridge on the outside of each of these cusps. The outside surfaces of these cusps of *Schoinobates volans* are generally concave, with only traces of the ridge. There is no distinct metastyle. In the stylar area of the tooth the ectoloph ridge stands more nearly vertical than in M^3 in *Pseudocheirus* and *Schoinobates.* All of these genera differ in this respect from *Phascolarctos* in which the ectoloph is nearly horizontal. The undescribed Kutjamarpu *Pseudocheirus* is most comparable to *Pseudokoala erlita* in this regard.

The protoconule and metaconule of *Pseudokoala erlita* are well developed but differ from those of all living *Pseudocheirus* in the following ways:

1. The protoconule is straight and is oriented in an anteroposterior direction rather than being curved. The transverse (anterior) portion is absent and the protoconule joins the anterior edge of the tooth.

2. The metaconule is not smoothly curved but has a right angle turn at its apex with one part (posterior) oriented antero-posteriorly and the other transversely. The metaconule of *Pseudocheirus herbertensis* approximates this right angle configuration and the posterior part is oriented straight antero-posteriorly.

3. Both protoconule and metaconule are low and rounded rather than sharp as in all living *Pseudocheirus*.

The enamel of the tooth is coarsely crenulate in the central basin. In this respect it is more like *Phascolarctos* and *Litokoala*, in which the crenulation is best developed in the basin between the paracone and metacone, than *Pseudocheirus archeri* and *P. herbertensis*. In these latter species the crenulation is found over much of the tooth and tends to radiate from the cusps.

There is a short, broad, rounded, irregular ridge on the inside of the ectoloph located half-way between the paracone and the mesostyle (at the transverse break in the tooth). It forms part of the crenulation of the crown of the tooth. It arises below the top of the ectoloph and ends in the valley between the paracone and metacone without joining any other ridges. Any of the first three molars of *Pseudocheirus archeri* has a small ridge (often two or three ridges) in this position, usually best expressed in M^1 or M^2 however, and the presence of these ridges and their connections to other ridges is variable even from left to right in the same dentition (FM 60919).

In *Pseudokoala erlita* a small elongate cuspule similar to that in *Litokoala* is also present in the median "V" of the ectoloph. It does not join any other ridges. Its long axis is oriented transverse to the tooth. A similarly located minute cuspule is sometimes found in *Pseudocheirus archeri* but it is variable in its occurrence between individuals, between the molars of one individual, and from side to side for any molar position.

In *Phascolarctos cinereus* the apparent homologues of these crenulate, ornamental ridges which come off from the ectoloph between the paracone and mesostyle are also well developed. The other cuspular development located just medial to the mesostyle in the bottom of the valley between paracone and metacone is more pronounced in *P. cinereus* in that it generally has the form of an elongate ridge which is usually tied to other more medially situated ridges in a variable manner.

NMV-P26400—L. M^4, Pl. VIII, Fig. A; Pl. VII, Figs. C, E

This tooth of *Pseudokoala erlita* consists of the central basin, and the adjacent portions of protocone, paracone, and metacone. Protocone is low, somewhat blunt, and not as strongly crescentic as that in all living *Pseudocheirus.* The ridges which give the crescentic form to the protocone extend anteriorly and posteriorly and form the internal and antero-internal margins of the tooth.

An open groove is present on the anterior side of the protocone. It extends from the region of the apex toward the paracone and gradually disappears. The protocone slopes gently toward the center of the tooth and ends in a row of poorly defined "bumps" which are separated from the rest of the tooth by a shallow groove. No living *Pseudocheirus* shows any of these features.

The paracone of M^4 has antero-internal and postero-internal ridges, as does the paracone of M^3, but they do not reach the base of the cusp. The internal face of the paracone is a flattened surface.

The metacone is broken off but was apparently present though reduced. It also appears to have been rotated out of line with the paracone, much as in *Pseudocheirus occidentalis, P. peregrinus,* and *P. herbertensis,* and seems to have been about as well developed relative to the other cusps.

The hypocone is barely discernible on the postero-internal margin of the tooth. It has about the same relative size as that of *P. occidentalis.* There is a single large central basin. The center of the central basin is raised and the enamel is coarsely crenulate as in the M^3. Most of the crenulation is found posterior to a line between the protocone and paracone. This feature gives a strikingly different appearance to these two areas of the basin. A very small protoconule is present antero-internal to the paracone. It is about four times longer than wide, oriented antero-posteriorly, and is rounded as in M^3.

NMV-P26399 (the M^3) and this specimen (NMV-P26400) have interdental wear facets which fit together so perfectly that these teeth must be the adjacent teeth of the same individual (Pl. VII, Figs. C–E). They were both found early in the processing of the matrix, coming from one of the first large batches of matrix to be worked.

PM 4588—Anterior half, left M_1

This specimen preserves paraconid, metaconid, and most of the protoconid. The tooth is broken away postero-lingually along the

axis of the crest that connects metaconid and hypoconid. It is worn and badly broken. The metaconid is only slightly higher than the paraconid, which may be due to wear. The metaconid and paraconid are joined by a strong ridge. The anterior part of the protoconid is joined by a worn ridge (metalophid) to the paraconid-metaconid ridge at about one-third of the distance forward from the metaconid. An anterior cingular ridge arises from a short crest extending anteriorly from the paraconid. It then extends labially and posteriorly and almost reaches the protoconid near the base of that cusp. This ridge cuts off a basin anterior to the protoconid. A large crenulation arises near the anterior edge of the basin and extends posteriorly to the middle of the basin where it dies out. This secondary ridge is separated from the cingular ridge by a narrow cleft. The anterolingual side of the tooth has an incipient cingular ridge which decreases in size anteriorly. It joins an anterior extension of the paraconid-metaconid crest (anterior to the paraconid) at the anterior tip of the tooth as does the external cingulum.

The protoconid is weakly crescentic in outline but not blade-like, though wear may be responsible for the rounding that it shows. The valley between the protoconid and the (missing) hypoconid is occupied by a coarse, round, pillar-like crenulation that lies close to the hypoconid crest. The posterior internal face of the protoconid has some coarse "bumps."

The labial face of the metaconid has a slight ridge which runs a very short distance externally before swinging sharply backward as it descends the posterior edge of the cusp. It is tied to a weak ridge which extends lingually from the protoconid. Both of these joined ridges show beveled wear facets. These two ridges and the metalophid combine to form a somewhat triangularly-shaped small basin.

The tooth does not have the deep valley between the paraconid and metaconid such as is present in *Perikoala palankarinnica* and which was mentioned by Stirton (1957a, p. 73, fig. 10). It resembles the M_1 of *Pseudocheirus archeri* in all of its basic morphology and in being heavily ornamented; but the details of the ornamentation are different. It shows the pseudocheirine tendency toward lateral compression of the trigonid. Also, the paraconid is present and the protoconid is relatively low. In the M_1s of *Phascolarctos cinereus* and *Perikoala palankarinnica* the paraconid is greatly reduced and the protoconid and metaconid are subequal and well separated.

Of the various species of *Pseudocheirus,* two (both in the subgenus *Pseudochirops*), *P. archeri* and *P. cupreus,* are much like

Pseudokoala, on the one hand, and the phascolarctines, on the other, than are any of the rest of the species of *Pseudocheirus* known to us. These similarities include size, basic morphology, and the extent of superficial ornamentation. Such similarities led us to err in our earlier report (Turnbull et al., 1965) where we noted the presence of a koala in the fauna based on NMV-P26399. We now believe this specimen to be a pseudocheirine rather than a phascolarctine (refer to comparisons given on pp. 27–29).

Measurements.—See Table 2.

TABLE 2.—Length and width measurements of the teeth of *Pseudokoala erlita* in the Hamilton fauna (in millimeters).

	M^3 (NMV-P26399)	M^4 (NMV-P26400)	M_T (PM 4588)
Length	6.9	5.3 (close)	—
Anterior width	— (5.0)*	— (4.6)*	2.5 (est. close)
Posterior width	4.6	— (3.8)*	—

* Estimated

Discussion.—The low lingual cusps of M^3 suggest that *P. erlita* was at a more primitive stage of dental evolution than any of the other known phascolarctids. The elongate, rectangular outline of M^3 corresponds with that of upper molars of pseudocheirines (which vary from nearly square to elongate) rather than with phascolarctines (which are consistently nearly square). The labial cusps also show a slightly more primitive condition than any modern pseudocheirine, to judge by the ectoloph development. The nearly vertical orientation of the ectoloph (especially the labial side of the stylar cusps) we take to be a somewhat primitive pseudocheirine feature, since all other known genera of the subfamily have less vertical ectolophs than *P. erlita*. Only the undescribed Kutjamarpu pseudocheirine shows as vertical an ectoloph, and it is thought to be older. In all phascolarctines the ectoloph is appressed against the crown surface and shows no tendency to stand off vertically. In the upper molars of pseudocheirines the angle the ectoloph makes with the occlusal surface ranges from a low of 50° for *Pseudocheirus archeri* to a high of 85–90° for *Pseudokoala erlita*. In the upper molars of phascolarctines this angle varies from 35–40° for *Phascolarctos cinereus* to 45° for *Litokoala kutjamarpensis*.

Cf. *Pseudokoala erlita*

Four other tooth fragments are very tentatively referred to *Pseudokoala*. Two of these, PM 4495 and PM 4496 (Pl. VIII, Figs.

C, D), differ from one another somewhat and both appear to be the posterior half of a stylar cusp. Both are unlike *P. erlita* in that they show distinct cingular mesostylar or metastylar "wings." Perhaps these were developed more on the more anterior molars as seems to be the tendency in most species of pseudocheirines. Both have crenulations in the valley that lead out toward the metastyle and run up onto the paracone. The crenulations are smaller and more elongate in PM 4496 than in PM 4495 which has large and bluntly rounded crenulations.

PM 4729 is such a small bit of tooth that its assignment is extremely dubious, yet it possesses a tantalizing amount of morphology. It consists of a single broken cusp with crenulations at the base. These crenulations and the apparent size of the cusp are the features that suggest that it may be referrable to *Pseudokoala*.

PM 4589, a postero-lingual corner of a right $M_{\overline{1}}$ which shows wear, is placed here with fewer misgivings than are the three last mentioned tooth fragments. It shows but little indication of the sort of crenulate enamel that typifies the best of the *P. erlita* materials. We believe that this is because the only parts preserved that are unworn are the posterior and labial sides, and that these areas were not crenulate in *P. erlita* lower molars. In *Pseudocheirus* (*Pseudochirops*) *archeri* these same areas lack crenulation although much of the occlusal surface is covered with crenulations. Presumably, lower molars of *P. erlita* had similarly uncrenulated sidewalls. Although not measurable, the tooth is large enough to be in the range for *P. erlita*, and is far too large to belong to either *P. marshalli* or *P. stirtoni* (see below). It has the lingually open valley behind the entoconid, typical for all pseudocheirines, but there is no trace of an entostylid ridge. If we are correct in this assignment, the lower molars of *P. erlita* apparently lacked an entostylid ridge (whether continuous or interrupted; see pp. 37–38) or else its expression followed a gradient along the tooth row, and the trait was gone on $M_{\overline{1}}$.

Pseudocheirus Ogilby, 1837

The genus *Pseudocheirus* is represented by more than 60 teeth or fragments of teeth, most of which fall into two species. One of these shows many similarities to species of *Schoinobates*. The association of the isolated upper and lower cheek teeth is based upon the correlation of characters associated in the upper and lower teeth of Recent species and upon functional and occlusal resemblances.

Pseudocheirus stirtoni[1] new species

Holotype.—Left M_{1-4} (NMV-P26401–P26404), associated on the basis of morphology, preservation, and the exact fit of the interdental facets (Plates IX–XII).

Referred material.—Upper Cheek Teeth: Left P^4 (PM 4549, Pl. XIII, Figs. A–C); right P^4 (PM 4590); right M^1s (or M^2s) (PM 4541, PM 4543, Pl. XIII, Fig. F; Pl. XIV, Fig. A); left M^1 (or M^2) (PM 4542, Pl. XIII, Figs. D, E); right M^2s (or M^3s) (PM 4422, Pl. XIV, Figs. B–D; NMV-P26410, Pl. XIV, Figs. E, F); left M^2 (or M^3) (PM 4500); right M^3 (or M^2) (NMV-P26411); left M^3 (or M^2) (PM 4479); fragment of an upper molar with paracone, parastyle, metacone, and metaconule (PM 4480); left M^2 or M^3 fragment consisting of metacone only (PM 4493); paracone of left M^2, M^3, or M^4 (PM 4746); paracone of left upper molar (PM 4747); protocone of left upper molar (PM 4467); left upper molar fragment with parts of paracone, metacone, and metaconule (PM 4749); and the protocone of a left upper molar (PM 4759).

Lower Cheek Teeth: Left P_4s (PM 4426; PM 4477, Pl. XII, Figs. C–E; PM 4548); left M_1 (PM 4474); right M_2 (or M_3) (PM 4424); left M_2 (or M_3) (PM 4545); anterior half right M_2 or M_3 (PM 4727); midsection of left M_2 or M_3 (PM 4550); labial half of a right M_1 (PM 4758); a left metaconid (PM 4753); and a left protoconid (PM 4468). The left P_4 (PM 4477) is probably (but not certainly) associated with the type on the basis of the fit of the interdental wear facets and preservation. It was recovered from the same lot of matrix as the teeth which constitute the type.

Diagnosis.—An animal near the size of *Pseudocheirus pygmaeus*, with molars slightly larger than those of that species (see *Measurements* and graphs). P^4 triangular with three laterally compressed labial cusps; the crest of the anterior cusp rounded in antero-posterior profile; anterior cusp close to center cusp but separated from it by a deep fissure rather than joined to it as in *Schoinobates*; central cusp with lingual ridge which extends from apex in a sigmoid curve to the back of the tooth near the postero-lingual corner; lingual cingulum present. All cusps of upper molars thin, sharp, and crescentic. Protoconule and metaconule well developed, sharp, and crescentic as protocone and hypocone. Posterior crest of protocone and anterior crest of hypocone not joined. Postero-internal ridges

[1] In honor of the late R. A. Stirton, an ardent student of the Australian Tertiary.

of paracone and metacone much stronger than antero-internal ridges which may be weak or absent. Protocone and hypocone with distinct median labial ridge. Cusps not joined by secondary transverse ridges. Enamel smooth and unornamented. The anterior edge of paracone of M^1 rounded, and not connected to the prominent parastyle by a ridge. $P_{\overline{4}}$ very short with two very closely spaced large twinned cusps in center of tooth. These cusps have a deep cleft between them. Posterior large cusp with two posterior ridges, the labial one running either postero-labially, labially, or antero-labially before turning posteriorly and joining a cuspule; the lingual one running posteriorly and lingually and sometimes ending in a cuspule. $M_{\overline{1}-\overline{3}}$ with well-developed entostylid ridge which is continuous with the entostylid. Anterior ridge of hypoconid wavy on all lower molars. Protoconid of $M_{\overline{1}}$ with distinct anterior and posterior crests. Well-developed metastylid connected to metaconid by a crest. Metastylid of $M_{\overline{1}}$ with well-developed posterior crest. $M_{\overline{1}}$ with distinct paraconid.

Descriptions.—The P^4 (PM 4590 and PM 4549, Pl. XIII, Figs. A–C) is a triangular tooth with three high, laterally compressed labial cusps. The anterior of these is rounded in its antero-posterior profile and is separated from the middle one by a deep fissure. The central cusp is more pointed and is joined to the posterior cusp by a thin sharp ridge. The posterior cusp is very compressed laterally and its posterior edge merges with the shelf-like posterior border of the tooth. The central cusp has on its lingual side a ridge which extends in a sigmoid curve dorsally and postero-lingually and fades out near the postero-lingual corner of the tooth. The lingual margin of the tooth is not preserved in either of the Hamilton specimens, but it is clear that there is a cingular basin lingual to the postero-lingual ridge of the central cusp. Thus, there are two posterior valleys as in *Schoinobates* and *P. lemuroides*. All other species of *Pseudocheirus* have only one posterior valley on the P^4. The tooth closely resembles the P^4 of *Schoinobates*. It differs in having the anterior cusp located closer to the central one and in not having a ridge joining them. Most of the species of *Pseudocheirus* have much more complicated P^4s than the fossil form. A few species of *Pseudocheirus*, *P. forbesi*, *P. pygmaeus*, *P. canescens*, *P. dahli* and *P. herbertensis*, have small and simple P^4s but none has the labial cusp as compressed as do these Hamilton specimens and *Schoinobates*.

The cusps of all upper molars are thin and sharp. The outer ridges of the paracone and metacone are crescentic except in M^1.

On either side of their junction (at the mesostyle) is a recurved, wing-like cingular ridge. The anterior one is usually the better developed of the two. The anterior edge of the paracone of M^{1} is rounded and not joined to the well-developed parastyle by a ridge (Pl. XIII, Figs. D–F; Pl. XIV, Fig. A). In this it is like the M^{1} of *Schoinobates volans*. The postero-internal ridges on the paracone and metacone are strong. The one on the paracone is nearly straight until it reaches the bottom of the cusp where it may turn sharply posteriorly, then labially before dying out. The ridge on the metacone is more curved and usually ends abruptly at the base of the cusp, but sometimes joins the posterior crest of the hypocone at the posterior edge of the tooth. The antero-internal ridges on the paracone and metacone are more reduced than in most species of the genus *Pseudocheirus* or are absent, especially on M^{1}. This is very similar to *Schoinobates*. The protocone is strongly crescentic. Its anterior crest forms the anterior edge of the tooth, and joins the parastyle in M^{1-3}. A small ridge is present on the anterior crest of the protocone, which forms a very rudimentary secondary selene. This is best developed on the M^{1}. A similarly-positioned, well-developed, additional selene characterizes the upper molars of all Recent species of the subgenus *Pseudochirops*. It is weakly developed in *Schoinobates* and many other species of the other subgenera of *Pseudocheirus*. The posterior crest of the protocone extends posteriorly and labially and ends in a valley between protocone and hypocone near the posterior end of the protoconule without joining another cusp. The hypocone is strongly crescentic. Its anterior crest runs forward and swings labially into the median valley where it disappears near the postero-lingual ridge of the paracone. The posterior crest of the hypocone forms the posterior border of the tooth and joins the posterior end of the ectoloph. The labial faces of the protocone and hypocone have distinct ridges which extend from the apices of the cusps to their bases where they disappear without joining the protoconule or metaconule. This is also the condition in *Schoinobates*. The protoconule and metaconule are well developed, and their antero-lingual faces are angular or ridged. The protoconule has its anterior end joined to the parastyle or paracone in M^{1}, and to the anterior edge of the tooth in M^{2-3} (Pl. XIV, Figs. D, F). It terminates posteriorly at (but not joined to) the anterior crest of the hypocone. Its apex is lined up with those of the paracone and the incipient additional selene on the anterior crest of the protocone. This is the usual pattern in those Recent species of pseudocheirines in which the additional selene is present (*Schoinobates*

and all species of *P.* (*Pseudochirops*)). The anterior end of the metaconule runs into the valley between the paracone and metacone and ends without joining any other ridge or cusp. The posterior end dies out labial to the postero-internal ridge of the metacone in the valley, usually near the posterior margin of the tooth. It does not join any other cusp or ridge. The apex of the metaconule is anterior to a line connecting metacone and hypocone. A small ridge, variable in length, is present at the posterior side of the base of the paracone of M^{1-2}. It parallels the posterior ectoloph ridge of the paracone and does not join any other ridge. A small lingual cingular cusp may be present between the protocone and hypocone of M^{2-3} (Pl. XIV, Figs. D, F). It is variable in size and exact location; it may lie exactly between those cusps, or more anteriorly against the base of the protocone. This cuspule shows similar variations in several Recent species of pseudocheirines.

The $P_{\frac{4}{4}}$ is a very short, triangular tooth with two large closely-spaced cusps in the center of the tooth. There is some variation in their spacing but they are always twinned and have a deep transverse cleft between them. The anterior large cusp is bulbous and rounded anteriorly. The posterior one is triangular with three ridges diverging from the apex. The antero-lingual ridge extends from the apex of the cusp to its base where it disappears. The postero-labial ridge runs postero-labially in PM 4426, labially in PM 4548, and antero-labially for a short distance then turns sharply posteriorly in PM 4477 (Pl. XII, Figs. D, E). In all three specimens this ridge ends in a cuspule at the postero-labial corner of the tooth. The postero-lingual ridge runs posteriorly and lingually and sometimes ends in a tiny cuspule. The $P_{\frac{4}{4}}$ is one of the most distinctive teeth in *Pseudocheirus stirtoni*. It is most like the $P_{\frac{4}{4}}$ of *Schoinobates* and *Pseudocheirus peregrinus*, but differs in being relatively smaller and shorter with its crowded, twinned, main cusps. Within *Schoinobates* it is more like *S. volans* than *S. minor* in the presence of two well-developed main central cusps and a developed postero-labial cusp. In *S. minor* the posterior of the main cusps, and the postero-labial cusp, are both very weakly developed being little more than sharp crests. In the reduction of the anterior cuspule it is more like *Pseudocheirus peregrinus*.

The lower molars have the general structure of *Pseudocheirus* molars. They resemble *P.* (*Pseudochirops*) molars in having a well-developed entostylid ridge in the valley between entoconid and hypo-

conid. This ridge is continuous with the entostylid. It is present on all lower molars except $M_{\bar{4}}$. In the living species of *Pseudocheirus* only *P. archeri* has this ridge on the $M_{\bar{4}}$. *Schoinobates* has a small entostylid ridge on $M_{\bar{1}-\bar{2}}$, which is not continuous with the entostylid, and none on $M_{\bar{3}-\bar{4}}$. The enamel is smooth and unornamented.

The $M_{\bar{1}}$ has a prominent protoconid which is not joined to any other cusp. The protoconid has well-developed anterior and posterior crests of which the posterior (Arrow #1, Plate IX, Fig. A) is the larger. *Schoinobates* and several Recent species of *Pseudocheirus* (*P. occidentalis, P. herbertensis, P. convolutor,* and *P. lemuroides*) have a comparable ridged independent protoconid on the $M_{\bar{1}}$. The metaconid is the largest cusp on the trigonid, and it is connected to the paraconid by a sharp ridge. A prominent metastylid is present which is almost as high as the metaconid and is joined to the metaconid by a ridge. It has a strong posterior crest which extends about half the distance to the entoconid and which overlaps lingually the anterior crest of the entoconid. The crest that connects the hypoconid and metastylid is wavy (Arrow #2, Pl. IX, Figs. A, C). It is interrupted in the middle by a small cleft in NMV-P26401 but not in PM 4474. The posterior end of the tooth is formed by a slightly wavy ridge which connects the hypoconid and the hypoconulid. The entostylid ridge is straight and extends from the entostylid to an imaginary line connecting the hypoconid and entoconid (Arrow #3, Pl. IX, Fig. A). There is a variably developed, procumbent anterior cingulum.

$M_{\bar{2}}$ and $M_{\bar{3}}$ resemble the $M_{\bar{1}}$ in the form of the talonid except for the terminal connection(s) of the anterior crest of the hypoconid (see area anterior to Arrow #2, Pl. IX, Fig. D; Pl. X, Fig. D). The anterior part of the teeth is somewhat different; there is no paraconid, and the protoconid has two crests. The anterior one extends straight anteriorly then turns about 45° lingually and almost joins the anterior crest of the metaconid at the anterior end of the tooth. The posterior crest is oriented transverse to the long axis of the tooth and ends at the posterior side of the base of the metaconid and either does not join it or joins by a very weak ridge. The anterior crest of the hypoconid of $M_{\bar{2}}$ (Arrow #2, Pl. IX, Fig. D; Pl. X, Fig. C) is wavy and is angled in much the same way as the anterior crest of the protoconid. It does not join the metastylid but joins the posterior crest of the protoconid close to the midline of the tooth. That of the $M_{\bar{3}}$ (Pl. X, Fig. D; Pl. XI, Fig. A) is only weakly wavy. The posterior crest of the metaconid on $M_{\bar{2}} - M_{\bar{1}}$ (Pl. IX, Fig. D; Pl. X, Figs. A, D; Pl. XI, Figs. A, D, E) slopes downward and joins a distinct but low metastylid lingual to the anterior crest of the ento-

conid. The metaconid and entoconid have rounded ridges which extend from the apices to the bases on both the lingual and labial sides. The entostylid ridge of $M_{\bar{2}}$ is large while that of $M_{\bar{3}}$ is short (compare Arrow #3, Pl. IX, Fig. D; Pl. X, Fig. D).

The $M_{\bar{4}}$ (Pl. XI, Figs. D, E) lacks the entostylid ridge as in all Recent *Pseudocheirus*, except *P.* (*Pseudochirops*) *archeri* in which it is well developed. The anterior crest of the protoconid is curved, not angled. The posterior end of the tooth is not flattened but is rounded. The junction of the anterior crest of the hypoconid with the posterior crest of the protoconid is located farther labially than in the other molars, as is generally true in the $M_{\bar{4}}$ of *Pseudocheirus*.

Measurements.—See Table 3.

TABLE 3.—Measurements of teeth of *Pseudocheirus stirtoni* (in millimeters)

		Length	Anterior Width	Posterior Width
$P^{\bar{4}}$	PM 4549	2.2	>1.2	>1.3
	PM 4590	2.2	>1.1	—
$M^{\bar{1}}$ (or $M^{\bar{2}}$)	PM 4541	>2.7	—	2.7
	PM 4542	3.2	~2.5	~2.4
	PM 4543	3.2	2.5	2.5
$M^{\bar{2}}$ (or $M^{\bar{3}}$)	PM 4422	2.9	2.7	2.5
	PM 4500	3.0	~2.7	2.5
	NMV-P26410	3.1	2.8	2.5
$M^{\bar{3}}$ (or $M^{\bar{2}}$)	NMV-P26411	2.9	2.6	2.1
	PM 4479	3.0	2.5	2.2
$P_{\bar{4}}$	PM 4426	2.0	1.0	1.3
	PM 4477	2.2	1.1	1.3
	PM 4548	2.1	1.1	1.2
$M_{\bar{1}}$	NMV-P26401	3.3	1.8	1.8
	PM 4474	3.2	1.8	1.8
$M_{\bar{2}}$	NMV-P26402	3.3	1.9	1.9
$M_{\bar{2}}$ (or $M_{\bar{3}}$)	PM 4424	3.1	1.6	1.9
	PM 4545	3.2	1.6	1.7
	PM 4727	—	1.7	—
$M_{\bar{3}}$	NMV-P26403	3.1	1.8	1.9
$M_{\bar{4}}$	NMV-P26404	3.5	1.8	1.5
	PM 4758	3.3	—	—

Discussion.—The genera *Schoinobates* and *Pseudocheirus* cannot be distinguished from one another solely on the basis of individual dental features. Even tooth proportions are inadequate for this, as can be seen from *Appendix* graphs A–D. However, *Schoinobates* does have a composite set of dental features that distinguish it. *P. stirtoni* shows many of the *Schoinobates* characterizing features (strong postero-internal and weak antero-internal ridges on paracone and metacone; rounded anterior edge of paracone on $M^{\bar{1}}$; double valley

on posterior end of P^4; and a short, morphologically distinct form of P_4) but it combines them with three other quite different features or sets of features. The first of these is the extensive continuous entostylid ridge development, such as is characteristic of all species of *P.* (*Pseudochirops*). (*Schoinobates* has the ridge, too, but it is separated from the entostylid.) Second is the failure of hypocone and protocone to join in M^{2-3}. The third of these different sorts of features is a new one, unique to *P. stirtoni* and the other new species of *Pseudocheirus* described below—the wavy form of the anterior ridge of the hypoconid.

Thus *P. stirtoni* is intermediate in dental morphology between *Pseudocheirus* and *Schoinobates*. Because of this, and because the most striking feature of *Schoinobates* (the gliding membrane) cannot be demonstrated for the fossil *P. stirtoni*, it is assigned conservatively to *Pseudocheirus*. Perhaps the strongest dental argument for an assignment to *Schoinobates* that can be made is one that relates to the pattern of change in tooth proportions from tooth to tooth (P_4–M_4), as can be seen in Graph E of the *Appendix*. In this regard *P. stirtoni* fits the *Schoinobates* pattern more closely than that of any of the subgenera of *Pseudocheirus* (*Petropseudes, Pseudochirops, Pseudocheirus* or *Hemibelideus*), although several species of *P.* (*Pseudocheirus*) also have a somewhat similar proportion pattern. Unfortunately, the sample sizes are small and until stronger evidence is forthcoming, based upon better samples, we prefer the more conservative assignment of the species to the broader genus *Pseudocheirus*.

Pseudocheirus marshalli[1] new species

Holotype.—Left M^4 (NMV-P26405), a nearly complete tooth showing moderate wear. Plate XV, Fig. B.

Referred specimens.—Fragment of a slightly worn left upper molar, probably an M^4, preserving metacone, metaconule and part of protocone (PM 4423, Pl. XVI, Fig. A); slightly worn left M^4 (PM 4587, Pl. XV, Fig. C); five upper molar fragments, three of which are each a left metacone (PM 4460, PM 4750, PM 4751), one a left hypocone and one a right hypocone (NMV-P26412, PM 4449); right P_4 nearly complete and showing a trace of wear (PM 4591, Pl. XV, Fig. A); unworn right M_4 (PM 4455, Pl. XVI, Fig. B); fragment of right M_4, including parts of protoconid and metaconid (PM 4461); slightly worn right M_2 (or M_4) fragment preserving hypoconid, ento-

[1] In honor of the late A. J. Marshall, founding professor of Zoology and Comparative Physiology, Monash University.

stylid and its ridge, and half of the entoconid (PM 4752); two partial left molars, either $M_{\bar{2}}$ or $M_{\bar{3}}$, one a talonid (PM 4425), the other a talonid with posterior half of trigonid (PM 4453, Pl. XVII, Fig. A); slightly worn right $M_{\bar{3}}$ (or $M_{\bar{2}}$) (NMV-P26413, Pl. XVI, Fig. C); a right $M_{\bar{4}}$ showing the beginning of wear on the anterior ridge of protoconid (PM 4476, Pl. XVII, Fig. B); and two fragments of lower molars, a right entoconid (NMV-P26414) and a left metaconid (PM 4462). It is probable that the $M_{\bar{3}}$ (NMV-P26413) and the $M_{\bar{4}}$ (PM 4476) belong to the same individual on the basis of wear and preservation, but the teeth had not been functional long enough for interdental facets to have formed.

Diagnosis.—An animal near the size of *P. stirtoni* or *P. pygmaeus*, with unornamented teeth about the size of those of the latter species. Primary cusps of trigon, trigonid, and also the hypocone, entoconid, and hypoconid are all more attenuated toward their apices, have sharper primary cresting and lack or have less secondary cresting than in *P. stirtoni*. $M^{\perp}$ with low, well-developed, pyramidal protoconule and metaconule, each with three straight ridges running from its apex. Paracone of $M^{\perp}$ rounded anteriorly, laterally compressed posteriorly to a blade-like form, and lacking internal ridges. Parastyle prominent, and metacone compressed and rounded posteriorly and lingually and with only traces of internal ridges. $P_{\bar{4}}$ elongate, triangular, and with two prominent midline cusps; the anterior large and rounded, the posterior smaller and ridged antero-posteriorly. A third cusp on the postero-labial corner connected to posterior end of ridged cusp by a diagonal ridge. The posterior end of tooth defined by a straight transverse ridge that extends from postero-labial cusp to postero-lingual corner of tooth. Entostylid ridge prominent on lower $M_{\bar{T}}$ but interrupted (i.e., not connected to entostylid); variable, but weak if present, in $M_{\bar{2}}$; absent in $M_{\bar{3}-\bar{T}}$. $M_{\bar{2}}$ and $M_{\bar{3}}$ with small entostylid and occasionally a trace of a hypoconulid. $M_{\bar{T}}$ with rounded, isolated protoconid. Posterior molars with thin blade-like metaconid and entoconid; posterior ridge of protoconid oriented perpendicular to line connecting those cusps. It is not angled or wavy as it usually is in the posterior molars of *P. stirtoni*. Anterior crest of hypoconid wavy but less so than in *P. stirtoni*.

Descriptions.—UPPER MOLARS: A left $M^{\perp}$ (NMV-P26405, Pl. XV, Fig. B) consisting of about three-fourths of a tooth with protocone and anterior half of hypocone missing, and one other upper molar fragment (PM 4423, Pl. XVI, Fig. A) which is probably an $M^{\perp}$, are

the only anterior molars of *P. marshalli* in the collection. The major cusps are attentuated toward the apex. The anterior end of the paracone is rounded and the posterior part is laterally compressed to a blade-like structure somewhat like that of the M^1 of *Pseudocheirus occidentalis*. There are no internal ridges on the paracone. The metacone is rounded on its lingual face and shows only traces of the internal ridges. There is a pronounced wing-like recurved cingular ridge, a part of a mesostyle, just anterior to the middle of the ectoloph. As in the M^1 of most species the ectoloph shows more flexure of its middle than would be expected in M^2 or M^3. The parastyle is large and separated from the paracone by a rounded groove that shows wear. The protoconule and metaconule are pyramidal in form. Each has a straight posterior crest oriented antero-posteriorly, and an anterior, labial crest oriented transversely. Each has a short straight ridge on the antero-lingual face. The anterior crest of the protoconule is very short and connects it with the base of the paracone. The anterior crest of the metaconule extends well into the valley between paracone and metacone. There is no secondary ridging in the valleys, and the enamel is smooth and unornamented.

The left M^4 (PM 4587, Pl. XV, Fig. C) is eloangted antero-posteriorly and is sub-triangular in outline. The three major trigon cusps are attenuated. The protocone is crescentic; its anterior ridge runs from the apex of the cusp diagonally forward and labially in an even arc which flattens out before reaching half-way across the tooth, and then runs straight labially along the front of the tooth to a small parastylar cusp. Paracone and metacone are laterally compressed and lack any internal cresting. Most of the ectoloph ridging is concentrated in the area between these cusps, where the ridges give off cingular wings which delimit a broad mesostyle. Lingual to the metacone at the postero-labial end of the posterior ridge of the protocone, there is a small hypocone. It is tied labially at its base to the base of the metacone, and more posteriorly by a continuation of the ridge that forms its axis to the base of the metacone near its posterior edge. Thus a minute basin is found between metacone and hypocone. There is a large and quite smooth-bottomed central basin with few features in it. The arm of this basin which extends broadly between the spread central ectoloph crests, has a slight valley or pit just lingual to the mesostyle. A similar valley lies immediately in front of the hypocone. A weak, straight antero-posteriorly oriented protoconule is present and ties straight to the front edge of the tooth. There is no trace of a metaconule.

LOWER TEETH: The P_4 is represented by an almost complete tooth (PM 4591, Pl. XV, Fig. A) with only the anterior portion missing. It is elongate, triangular and has three cusps preserved. The anterior of these (1 in Pl. XV, Fig. A) is the largest and appears to be the homologue of the main cusp of the P_4 of *P. occidentalis* (PM 4765) in which it is located just anterior to the center of the tooth. It is rounded with two weak ridges on its anterior face that extend anteriorly to the broken edge of the tooth. There was probably a small anterior cusp as on the P_4 of most living species of *Pseudocheirus*. Posterior to the large rounded cusp is a smaller median cusp (2 in Pl. XV, Fig. A) with antero-posterior ridging. This ridge turns abruptly postero-labially at the posterior end of the cusp and joins another cusp (3 in Pl. XV, Fig. A) on the postero-labial corner of the tooth. From this cusp a ridge extends across the posterior end of the tooth and ends at the postero-lingual corner. The tooth is quite similar to the P_4 of *P. occidentalis* and *P. lemuroides* in the basic arrangement of the cusps. However, the ridge that connects the two posterior cusps runs down the posterior side of the compressed median cusp rather than off from its labial side. Also, the posterior end of the tooth is oriented more transversely with respect to the long axis of the tooth.

The M_1 (PM 4455, Pl. XVI, Fig. B), is similar to, and is only slightly smaller than, that of *P. stirtoni*, but differs in two fundamental ways. The protoconid, which is not joined to any other cusp, is not compressed laterally as in *P. stirtoni*, but is a simple oval pillar. Also, the entostylid ridge is not continuous with the entostylid (a *Schoinobates* characteristic) as it is in *P. stirtoni*. Neither of these two diagonostic features shows variation in the M_1 of any of the living species, and thus it seems unlikely that PM 4455 could be simply a variant of *P. stirtoni*. Because of the slight size difference, the major cusp height and attenuation, and the character of the development of the entostylid and its associated ridge which shows a gradient descending from M_1 to M_4 (as in *Schoinobates*), *P. marshalli* is distinguished from *P. stirtoni*.

The posterior lower molars (PM 4425, PM 4453, NMV-P26413, PM 4476) are also similar to those of *Pseudocheirus stirtoni* but have no more than a trace of an entostylid ridge. The M_3 (NMV-P26413, Pl. XVI, Fig. C) typifies them all. The metaconid and entoconid are very thin and blade-like and lack prominent rounded ridges on the labial faces. There is a weak entostylid, and while this specimen lacks a hypoconulid, a trace of one can be seen on PM 4425 and PM 4453. The posterior crest of the protoconid (except in M_4) is

oriented perpendicular to a line connecting metaconid and entoconid instead of slightly obliquely as is usually the case in *P. stirtoni*. It does not join either the metaconid, the anterior crest of the entoconid, or the metastylid. The anterior crest of the hypoconid has a less pronounced labial loop where it joins the posterior crest of the protoconid than it does in *P. stirtoni*, and is somewhat less wavy than in *P. stirtoni*.

The $M_{\bar{4}}$ of *P. marshalli* (PM 4476, Pl. XVII, Fig. B) has a thinner metaconid and entoconid than does that of *P. stirtoni*. It is slightly smaller than the $M_{\bar{4}}$ of *P. stirtoni* and lacks the low ridges on the labial face of the metaconid.

Measurements.—See Table 4.

TABLE 4.—Measurements of teeth of *Pseudocheirus marshalli* (in millimeters)

		Length	Anterior width	Posterior width
M^1	NMV-P26405	3.4	—	—
M^4	PM 4587	2.8	2.3	1.4
$P_{\bar{4}}$	PM 4591	—	—	1.5
$M_{\bar{1}}$	PM 4455	3.0	1.4	1.5
$M_{\bar{2}}$ (or $M_{\bar{3}}$)	PM 4425	—	—	1.9
	PM 4453	—	1.7 est.	1.8
$M_{\bar{3}}$ (or $M_{\bar{2}}$)	NMV-P26413	3.0	1.6	1.7
$M_{\bar{4}}$	PM 4476	3.1	1.7	1.5

Discussion.—*P. marshalli* shows fewer resemblances to *Schoinobates* than does *P. stirtoni*. It resembles *Schoinobates* in the rounded anterior edge of the paracone of M^1 and in the interruption of the entostylid ridge in $M_{\bar{1}}$ and $M_{\bar{2}}$, and its absence in $M_{\bar{4}}$. This ridge shows a steeper gradient in *P. marshalli* in its degree of expression from $M_{\bar{1}}$ to $M_{\bar{4}}$ than in *Schoinobates*. In other features it resembles one or more living species of *Pseudocheirus*. Neither *P. stirtoni* nor *P. marshalli* shows any decidedly generalized characters such as might suggest either one to be the ancestor of a living species. Neither one appears to be more primitive or more specialized than most of the Recent species. *P. marshalli* fits best into the subgenus *P.* (*Pseudocheirus*) (Tate, 1945B).

Pseudocheirus sp. (incisors and other fragments)

Material.—Two left $I_{\bar{1}}$s (PM 4472, Pl. XVII, Fig. C; NMV-P26415, Pl. XVIII, Fig. A); tips of two right $I_{\bar{1}}$s (PM 4427, PM

4428); section of a right $I_{\overline{1}}$ at base of enamel (PM 4584); distal part of left $I_{\overline{1}}$ (PM 4551); root of $I_{\overline{1}}$ (PM 4585); and the following cheek tooth fragments: a protocone or hypocone (PM 4488); a metaconid (PM 4463); eight isolated fragments (PM 4596); an entoconid, probably an $M_{\overline{1}}$ (PM 4464); a left metaconid (NMV-P26416); a worn, hypoconid? (PM 4594, Pl. XXIX, Fig. F); a hypoconid (PM 4754).

Description.—The $I_{\overline{1}}$s are very close to the size of the $I_{\overline{1}}$ of *Pseudocheirus pygmaeus* and show approximately the same longitudinal curvature and dorso-ventral flattening. They differ from the $I_{\overline{1}}$ of *P. pygmaeus* and all other living species of *Pseudocheirus* in being relatively narrower and in having a more pronounced bulge on the dorsal surface at the enamel line. The lateral cutting edge is thin and blade-like as in all living species of *Pseudocheirus*. The profile of the lateral cutting edge is straight, not strongly sigmoid as in most species of the subgenus *Pseudochirops*. The medial interdental facets tend to truncate the medial dorsal ridge at the distal end of the tooth. This is less pronounced than in the living species of *Pseudocheirus* and more like the condition found in the $I_{\overline{1}}$ of *Petaurus*. There is no way to assign the incisors to either of the named species of *Pseudocheirus* of the Hamilton fauna, but it seems likely that they probably belong to one of those species. There are no differences between the $I_{\overline{1}}$s to indicate that more than one species is represented. These incisors show in their shape and the lesser truncation of the medial dorsal ridge, a condition more primitive than is seen in any Recent species of *Pseudocheirus*.

Family Macropodidae

Subfamily Potoroinae

Genus and sp. indet., near *Aepyprymnus*

Material.—Metacone of a left upper molar (PM 4492), with the posterior cingulum and a small part of the hypocone preserved. Plate XVIII, Fig. B.

Description.—This specimen is about the size of the metacone in the upper molars of *Aepyprymnus rufescens*. The cusp is broader and more bulbous than in *A. rufescens*, particularly the lingual part. There is a poorly defined wear facet on the anterior side which produces what little cresting there is to the low transverse ridge, just posterior to the center of the cusp. The same pattern of wear is found on metacones of *A. rufescens*. The posterior cingulum (arrow, Pl. XVIII, Fig. B) is short, heavy, and rounded, and shows a small

wear facet near the broken edge of the tooth fragment. The break surface truncates the extreme postero-labial edge of the hypocone and its pulp canal where the cingulum joins that cusp. The cingulum joins the metacone more lingually along its posterior face than in *A. rufescens* in which it extends onto the labial side of that cusp. The posterior cingular basin thus formed is almost circular (slightly crescentic) and is located at the postero-lingual corner of the metacone. This basin in *A. rufescens* is elongated transversely to the tooth and extends across the breadth of the tooth. PM 4492 differs from the large potoroo ("cuscus") of Gill (1953b, 1957), which was described by Stirton (1957b) and has since been redescribed and identified by Ride (1964), in its smaller size and more bulbous metacone, and the less prominent, less ridged metaloph.

Discussion.—This specimen is closer to *Aepyprymnus* than to any other known genus of the Potoroinae, but the differences listed above suggest that better material may necessitate the establishment of a new genus.

Genus and sp. indet., near *Hypsiprymnodon*

Material.—Anterior half, right M^{1} (PM 4575, Pl. XVIII, Fig. C).

Description.—This Hamilton tooth is unworn, sharply crested, and is quite similar to, and about the size of, the M^{1} of *Hypsiprymnodon moschatus* (FM-60953). It has a rounded, columnar ridge running the full height of the protocone, and sharp angular ones at the antero-lingual (parastyle) and antero-labial corners of the procingulum. The procingulum is thus squared off anteriorly; it is connected to the protocone by an uninterrupted angular ridge, and to the paracone by a similarly sharp ridge which is nicked by a noticeable notch. Rootward from this notch, on the labial side of the tooth, is a depressed area. As a result, the antero-labial end of the procingulum has the appearance of a parastylar cusp. There is a short lingually-curved posterior ridge to the paracone which fades out without joining a crest from the metacone. A sharp protoloph is a prominent feature of the tooth. It has a minute cleft at its midpoint and it is weakly expanded just labial to this cleft. Postero-labial to the paracone, on the labial side of the tooth near its base, there is another low ridge that is sharpest away from the apex of the cusp and disappears about half-way from base to apex. The posterior crest of the protocone must have reached to, and, judging by the break surface, was probably connected with a crest from the hypocone.

The overall shape of the tooth in crown view is very similar to that of *Hypsiprymnodon moschatus* because of the extensive development of the procingulum, with a straight anterior edge. It is also similar in having the well-developed parastyle. It differs in having a postero-labial ridge on the labial side of the paracone, in lacking the posterior and anterior bulges on the labial segment of the protoloph, and in lacking a pitted enamel surface.

The only other genus of potoroine in which there is a tooth at all comparable is *Aepyprymnus*. In this genus the M^2 shows most of these features, but the ridges are less sharp and the procingulum is more rounded.

Sp. indet., with similarities to *Potorous* and *Propleopus*

No additional representatives of the original potoroine find (Gill's and Stirton's "cuscus") have turned up in our collection. Hence each of these potoroine taxa is presently represented by a single tooth or fragment. By contrast, *Dorcopsis* is common. It usually is put in the Macropodinae, but here following authority (Woodbourne, 1967; Stirton et al., 1968) we put it in Potoroinae.

Dorcopsis Schlegel and Müller, 1839–1844

Dorcopsis sp. indet.

Material.—UPPER TEETH: Posterior third of a right P^4 (PM 4436, Pl. XIX, Figs. A–D); complete unworn right molar (NMV-P26417, Pl. XXI, Figs. A–D); complete left molar with good interdental facets, and showing enough wear that the enamel of protocone and paracone is breached, exposing dentine (PM 4433, Pl. XX, Figs. A–E); complete unworn right molar (PM 4434, Pl. XXII, Figs. A–D); the anterior half of a right molar (PM 16807); two fragments of left molars that may have been adjacent teeth in the same mouth to judge by fit of interdental facets, preservation, and wear—(PM 4485) a worn left metacone, and (PM 4431) a left anterior half tooth with procingulum, protocone, paracone, and protoloph; anterior quarter of a left molar, somewhat worn, with well-developed interdental facet and with procingulum and anterior half of protocone, paracone and protoloph preserved (PM 4484); anterior half right molar showing beginning of wear on protoloph, and possessing an unusual, small accessory cuspule postero-labially to the paracone (PM 4570); two molar fragments, each consisting of the labial side of the median valley—a right (PM 4572), which also has most of the paracone and procingulum preserved, and a left (PM 4573); a fragment of the an-

terior face of a left metacone (PM 4755); and a fragment consisting of parts of a protocone and procingulum of a right upper molar (PM 4713).

LOWER TEETH: Nearly complete slightly worn right molar (probably $M_{\overline{3}}$ or $M_{\overline{4}}$) lacking tip of protoconid and half the hypoconid (PM 4565, Pl. XXIII, Fig. A); anterior half right molar (NMV-P26418); anterior half right molar (PM 4482).

Descriptions.—The $P^{\underline{4}}$ fragment (PM 4436, Pl. XIX, Figs. A–D) closely resembles the posterior part of the $P^{\underline{4}}$ of *Dorcopsis mülleri* (FM-8379) from New Guinea in both size and morphology. The outer blade is thin with a flat labial surface up to the posterior ridgelet, where it is broken. There is a postero-lingual cusp which is joined to the outer blade by two ridges. The anterior of these extends antero-labially to the external blade. The posterior ridge extends posteriorly, then turns labially, decreases in height and joins the outer blade at the base of the tooth. These two ridges delimit a posterior basin which has a narrow opening posteriorly. A third ridge extends lingually, then anteriorly from the postero-lingual cusp. It decreases in height and forms a low shelf along the lingual side of the tooth. A small tubercle is located on this shelf at its anterior end, opposite the posterior ridgelet of the outer blade. The $P^{\underline{4}}$ of *D. mülleri* lacks this tubercle. The Hamilton specimen is not as high-crowned as the $P^{\underline{4}}$ of the Recent *Dorcopsis*. *Wallabia bicolor* has the posterior basin elongated and oriented more or less parallel to the long axis of the tooth, and has a relatively more massive external blade. *Dendrolagus* differs from the Hamilton specimen in having no posterior basin, and in its more massive and irregular external blade.

The upper molars are sufficiently alike one another that a general description of them may be given and the variations noted. The protoloph and metaloph are sharp when unworn, and are V-shaped or curved with the concavity facing posteriorly. The paracone and metacone have well-developed anterior and posterior crests. The anterior crest of the paracone joins the procingulum. The posterior crest of the paracone is always straight and extends in a slightly lingual angle from the apex to the base of the cusp. The anterior crest of the metacone shows considerable variation: it may be straight (NMV-P26417) or curved (PM 4433, PM 4434, PM 4485) and may (NMV-P26417, PM 4433, PM 4434) or may not (PM 4485) reach the base of the cusp. In those teeth in which these crests between paracone and metacone reach the central valley, they may (PM 4433) or may not (NMV-P26417 and PM 4434) be joined. In those in

which the crests do not reach the central valley there is a U-shaped notch between the cusps.

Variations similar to these are found as a graded series (from connected crests anteriorly to interrupted crests posteriorly) along the tooth rows of many Recent macropodids. The shape, relative size, and orientation of these crests are more like the Recent *Dorcopsis* than any other macropodid, but the gradient along the tooth row is somewhat steeper. The paracone and metacone of *Wallabia bicolor, Dendrolagus lumholtzi, Thylogale brunii, T. stigmatica, T. billiardieri,* and *Setonyx brachyurus* have these crests or ridges, but they differ from those of *Dorcopsis* and the Hamilton species in various ways. In *Dendrolagus* they are much reduced. In *W. bicolor* these two crests of M^1 and M^2 are joined in the median valley and have a short segment parallel to the long axis of the teeth. In M^3 and M^4 of that species the crests are absent or weak. In all species of *Thylogale* the anterior crest of the metacone is either absent or is reduced to a low ridge. In *Onychogale* the metacone lacks an anterior crest. In *Setonyx* these ridges have a smooth curve from apex to central valley, and those of the anterior molars join while those of the posterior molars do not.

The midlink of the upper molars in the Hamilton species arises on the posterior side of the protocone below the apex and extends postero-labially to the central valley, then turns posteriorly and joins the metaloph at its midpoint. It does not reach the crest of the metaloph. A short labial spur may be present on the midlink in the central valley (PM 4434, Pl. XXII, Fig. C). This is either absent or only slightly developed in the Recent species of *Dorcopsis*. Low on the labial side of the crown, postero-labial to the protocone, there is a diagonal bulge (in all but one specimen) or ridge (PM 4570) as in upper molars of the Recent *Dorcopsis* and *Dorcopsulus*. In these Recent forms there is a marked gradient to the expression of this trait, from strongest on the anterior molars to weakest on the posterior.

The procingulum is prominent with the straight anterior edge parallel to the protoloph. The anterior crest of the paracone joins the anterior ridge of the cingulum. The cingulum has a square antero-labial corner, and does not reach the lingual edge of the teeth. A forelink is absent, being represented by a slight bulge. It is present though much reduced in the Recent species of *Dorcopsis*. The postcingulum is crescentic. It leaves the apex of the hypocone, extends lingually and rootward, and then swings up onto the apex of the metacone. This is similar to the postcingulum in Recent *Dorcopsis*.

The postcingulum is greatly reduced in *W. bicolor*, and in M^{1}–M^{3} in *Thylogale, W. eugenii,* and *Onychogale frenata.* There is a well-developed cingular shelf labially at the central valley, as in *D. mülleri.* (*Dorcopsulus* lacks this shelf.) There is no sign of the pitting such as is found in the central valley and anterior and posterior cingular basins of *D. hageni.*

The one nearly complete lower molar of *Dorcopsis* sp., in the Hamilton fauna (PM 4565, Pl. XXIII, Fig. A) is relatively wide, like the molars of the Recent *D. hageni* and *D. mülleri,* in contrast to most species of *Wallabia.* The protolophid and hypolophid either have the form of very flat V's with the concave sides anterior or are straight. The metaconid and entoconid each have a prominent anterior crest oriented at a right angle to the corresponding protolophid or hypolophid, as in the molars of Recent *Dorcopsis.* These crests are between one-quarter and one-third the length of the cross lophs. They die out on the lower parts of the cusps. The crests are developed to about the same degree in *D. mülleri* (FM-8379) and *D. hageni* (FM-31859). They are present but are relatively much shorter in *Dendrolagus lumholzi* and *Thylogale billiardieri.* The apex of the hypoconid is not preserved in PM 4565, so the nature of its connection with the midlink is uncertain. The anterior part of the midlink is located at the middle of the tooth and is parallel to the long axis of the tooth. It seems to have turned sharply lingually then anteriorly after leaving the hypoconid. The midlink is interrupted by a narrow cleft at the middle of the transverse valley in PM 4565. The anterior quarter of the midlink appears to be a posterior spur from the protolophid. The midlink is interrupted in *D. mülleri* and *D. hageni* but in the latter species it is more like the fossil. The midlinks in both Recent species of *Dorcopsis* are located more labially than in the fossil and are not parallel to the long axis of the tooth.

The junction of the forelink (paralophid) with protoconid is not preserved in PM 4565 as it is in NMV-P26418 and PM 4482—in both of which the link is located labial to the mid-axis of the tooth. In the latter it runs as a crest diagonally forward from the protoconid apex for nearly half its length before swinging to an antero-posterior alignment. In NMV-P26418 it runs almost straight diagonally to the procingulum. In PM 4482 the procingulum is rounded and more procumbent than in the others. In *D. hageni* and *Dorcopsulus* (AMNH 157267) the anterior cingulae of the anterior lower molars are more procumbent than those of the posterior molars. The anterior part of the forelink in PM 4565 is located close to the midline

of the tooth and is nearly, but not quite, parallel to the long axis of the tooth. It joins an anterior cingular ridge at the mid-point of the anterior edge of the tooth. This junction is located more labially in both NMV-P26418 and PM 4482 and in the Recent species of *Dorcopsis*. The anterior cingular ridge in PM 4565 and NMV-P26418 swings labially in a smooth curve and merges with the base of the protoconid before reaching the labial edge of the tooth. In PM 4482 there is a small vertical groove between the protoconid and the labial end of the procingulum. The base of the protoconid has a swelling adjacent to this groove. The lingual segment of the procingulum extends lingually, then turns abruptly posteriorly and joins the base of the metaconid before reaching the lingual edge of the tooth. There are no pits in the enamel at the bases of the anterior faces of the protolophid and hypolophid as in *D. hageni*.

The Hamilton *Dorcopsis* material shows many resemblances to *Dorcopsoides fossilis* from the Alcoota fauna of central Australia (Woodburne, 1967), particularly in the parastylar ridge and small lingual cingulae of the upper molars, the vertical lophids, similar structure and position of fore-link and mid-link of the lower molars, the absence of a lingual cingulum, and a slight development of a labial cingulum in the lower molars. It is also similar in the relatively low crown height of the teeth. The metacone height of M^2 of *Dorcopsoides* ranges from 2.8–3.8 mm.; that of one M^3 is 2.8 mm. Metacone heights of the two measurable upper molars of the Hamilton *Dorcopsis* are 2.3 and 2.5 mm.

The *Dorcopsis* from Hamilton differs from the Alcoota species in: smaller size; the presence of a posterior basin and a lingual tubercle ahead of the postero-internal cusp on P_4; absence on upper molars of mesostyle and of facets on paracone and metacone; absence on lower molars of longitudinal crests on protoconid and hypoconid; metaconid and entoconid not conical; and the anterior crests on metaconid and entoconid are better developed.

The Hamilton *Dorcopsis* also shows similarities to a specimen from the Awe fauna of New Guinea which was referred by Plane (1967) to the genus *Dorcopsis*. The Hamilton material differs in: smaller size; absence of spurs on the paracone and metacone which meet at the labial end of the median valley; absence of mesostyle; relatively narrower upper molars; and possibly weaker mid-links. In addition, the Hamilton specimens do not show strong posterior tapering, although this may result from the lack of an M^3 or M^4 in the Hamilton material. Woodburne (1967) has suggested that this

New Guinea species may be closer to *Dendrolagus* than to the *Dorcopsis–Dorcopsoides* group.

Measurements.—See Table 5.

TABLE 5.—Measurements of teeth of *Dorcopsis* sp. from the Pliocene, Grange Burn, Hamilton fauna (in millimeters)

	Length	Anterior width	Posterior width
Right P^4 (PM 4436)	—	—	3.9
Right upper molar (NMV-P26417)	5.5	4.7	4.2
Left upper molar (PM 4433)	5.4	4.4	4.5
Right upper molar (PM 4434)	5.8	4.3	4.4
One-half left upper molar (PM 4431)	—	4.4	—
One-half right upper molar (PM 4570)	—	4.1	—
One-half right upper molar (PM 16807)	—	4.3	—
Right lower molar (PM 4565)	5.4	3.9	3.8
Anterior one-half right lower molar (PM 4482)	—	3.7	—
Anterior one-half right lower molar (NMV-P26418)	—	3.8	—

Discussion.—We believe that the *Dorcopsis* sp. materials described above represent a new species, but in spite of the fact that four of them are complete teeth and that several others are very informative partial teeth, we are not naming a new taxon for we cannot be certain about associations. Most of the diagnostic features, which appear to be consistent for the Hamilton specimens may be found individually, or in other combinations, elsewhere within the macropodines. As examples of these diagnostic features, all of the upper molars preserving the pertinent parts have:

1. Paracone and metacone with antero-posterior cresting (except one which shows the other features the batch has in common);
2. Straight procingulum with a strong tendency to square off the antero-labial corner of the tooth so that the outer corner of the cingulum is even with the paracone and metacone;
3. Straight posterior crest of paracone;
4. Tendency in some teeth (presumably in the anterior molars) for paracone and metacone crests to join, forming a labial auxilliary "midlink";
5. Absence of forelink.

Fewer diagnostic features are to be found in the lower molars. In them:

a. the metaconid and entoconid both have strong anterior crests that hook forward from the lingual end of the lophid, and

b. the procingulum is notably broad rather than being narrowly sharp or pointed.

On the basis of the parts of the animal available to us, the Hamilton *Dorcopsis* species appears to be just as advanced as any Recent species of the genus.

See also further discussion in section on *Thylogale* (pp. 59–62).

Subfamily Macropodinae

There are 33 teeth or tooth fragments which are clearly assignable to this subfamily. Eighteen of these teeth can be assigned to the genus *Thylogale*. On the basis of size and general morphology, the remainder (15 teeth) probably represent two or three taxa. These include *Protemnodon* as well as one or more other taxa whose generic affinities are uncertain.

Thylogale Gray, 1837

Thylogale sp. indet.

Materials.—UPPER TEETH: A worn partial left I^2 (PM 4733, Pl. XXV, Fig. C); an unworn partial right I^3 (PM 4731, Pl. XXV, Figs. A, B); a complete, unworn right molar, probably M^2, M^3 or M^4 (PM 16802); metaloph of an unworn left molar, probably M^2, M^3 or M^4 (NMV-P26421); the unworn hypocone of a left molar, probably M^3 or M^4 (PM 4452); and a worn left hypocone (PM 4574).

LOWER TEETH: Three left I_1s, each only slightly worn (PM 4444, Pl. XXV, Fig. D; NMV-P26419; PM 16805); posterior two-thirds of a worn right P_3 or P_4 (PM 4562, Pl. XXVII, Fig. A); a complete unworn right dP_1 (PM 4438, Pl. XXVI); the antero-labial quarter of a right dP_4 (PM 4586); the posterior half of a left dP_4 (PM 4483); an unworn, complete right M_1 (PM 4564, Pl. XXIII, Figs. B–E); two moderately worn complete teeth, probably M_2s (or M_3s), (NMV-P26420 and PM 4576, Pl. XXIV, Figs. A–D); the unworn, anterior half of an M_3 or M_4 (PM 4432, Pl. XXIV, Figs. E and F); and a worn antero-lingual corner of an M_3 or M_4 (PM 4451).

Descriptions.—UPPER TEETH: The incisors are represented by the lateral sides of two teeth, a right I^3 (PM 4731) and a left I^2 (PM 4733). The I^2 has a triangular lateral surface which is gently convex from root to crown. Very gentle rounded pillars are present at the anterior and posterior ends of the tooth. It is similar to the I^2 of *T. billiardieri* but the pillars are less obvious and the tooth is slightly smaller. It is at about the same stage of wear as a specimen of *T. billiardieri* (FM 81526).

The right I^3 preserves the lateral side of the tooth anterior to the notch on the outside of the tooth. The portion of the tooth which is preserved is gently convex from root to crown. The labial surface has a broad, low, rounded pillar running from the crown toward the root in the anterior quarter of the specimen. It is very similar to the anterior part of the I^3 of *Thylogale billiardieri* in which the notch is located near the posterior end of the tooth. The blade, which is labial to the median groove on the crown of the tooth, is proportionately lower than in *T. billiardieri*.

The complete right upper molar (PM 16802) is about the size and shape of the M^2 or M^3 of *T. billiardieri* or those teeth and M^4 of *T. stigmatica*. The lophs are concave posteriorly and are gently rounded. The procingulum is broad and is connected to the paracone by the sharp anterior crest of that cusp. There is no trace of a forelink. The paracone also has a sharp posterior ridge that extends rootward and slightly lingually almost to the bottom of the transverse valley where it swings abruptly lingually and disappears. The metacone is ridged in much the same way as the paracone. Its anterior ridge is very prominent near the apex of the cusp and gradually dies out as it approaches the transverse valley, thus failing to form a complete labial link. The bottom is tightly V-shaped where it runs between this ridge and the posterior ridge of the paracone. The posterior ridge of the metacone is sharp near the apex of the cusp, but becomes rapidly reduced midway to the base of the tooth. In crown view it is a smooth continuation of the arc of the metaloph. The tip of the protocone is broken away. The midlink arises on the postero-labial side of the protocone at a point about one-third the distance from the apex to the base and extends to the middle of the tooth. There it is met by a nearly equal contribution from the metaloph. The central part of the midlink rises to about one-half of the height of the lophs and is clefted in its upper part. The postcingulum is sharp, higher on the hypocone than the metacone and isolates a narrow V-bottomed cingular basin that opens labially.

This tooth resembles the M^2 and M^3 of *T. billiardieri* in morphology more than those of any other macropodid, but differs in several minor ways. The procingulum is relatively broader than those of the lower molars of *T. billiardieri*, the midlink is less kinked, and the metaloph is more curved.

It differs from M^2 and M^3 of *T. brunii* and *T. stigmatica* in being more elongate and in having no trace of a forelink. It also differs from those teeth in *T. billiardieri*, as well as in the above-named spe-

cies, in the extensive development of the antero-labial crest of the metacone.

Another specimen (NMV-P26421) consists of the metaloph. It is similar to PM 16802 in every respect except the extent of the ridging on the posterior face of the metacone and the minor development of pitting on the posterior face of the metaloph. The posterior ridge of the metacone extends to the cingulum.

The other two upper molar fragments are left hypocones. The larger (PM 4452) is slightly larger than its counterpart in the posterior molars of *T. billiardieri*, and resembles them in the lateral tapering of the lophs, a weak crest to the postcingulum, and a midlink that almost reaches the crest of the metaloph.

The hypocone of the smaller upper molar fragment (PM 4574) is about two-thirds the size of the other. The loph narrows laterally toward its crest. It is quite worn so the original height of the connection of the midlink and the metaloph is uncertain. It shows no trace of a posterior ridge leading to a postcingulum. In this last character it is like the M^2 or M^3 of *Thylogale stigmatica*.

The best two lower incisors are virtually identical to those of *T. billiardieri* (FM 81526). They are lanceolate, broad, and gently curved along the long axis. The transverse curvature on the ventro-labial side extends through an arc of almost 90°. The central axial bulge is low and rounded, and is flanked on either side by a slightly recurved ridge. The ventro-medial ridge is slightly broader than the dorso-lateral one. The line that marks the rootward limit of the enamel on the lingual surface is W-shaped, with the enamel extending farther rootward along the edges and with a spur of enamel running rootward along the center of the tooth. On the labial side of NMV-P26419 near the dorsal ridge there is a U-shaped line marking the rootward extent of the enamel. The pattern of the enamel line on the lingual surface is like that in *T. billiardieri* (FM 81526). PM 16805 adds nothing to our knowledge that is not conveyed by the others.

The lower $P_{\overline{3}}$ or $P_{\overline{4}}$ (PM 4562, Pl. XXVII, Fig. A) consists of the posterior two-thirds of a worn blade-like tooth that has a decided but gentle lingual turn at its posterior end just in front of the last cuspule. There are three cuspules preserved, but it is doubtful that the blade was truly serrate in character when unworn, for the ridges and grooves are broad. There is a small, well-defined triangular interdental facet on the posterior end. This facet is situated labial to the sharp postero-lingual ridge that continues on from the axis of the

tooth at the apex of the last cuspule. The ridge runs steeply down to the base of the tooth. The tooth compares best with $P_{\overline{3}}$ or $P_{\overline{4}}$ of *Thylogale billiardieri*. It is larger than the $P_{\overline{3}}$ of that species (FM 81526) and the posterior inflected turn of the crest is slightly less marked.

It resembles these teeth in *T. stigmatica*, too, but is nothing like those of *T. brunii* with their high, well-formed distinct cusps. There are some similarities to the $P_{\overline{3}}$ and $P_{\overline{4}}$ of *Setonyx brachyurus* and *Dorcopsis mülleri* but these are not nearly as close as *Thylogale billiardieri*.

The description of the $dP_{\overline{4}}$s (PM 4438, PM 4483, PM 4586) is based on the complete tooth (PM 4438, Pl. XXVI) and, except as otherwise noted, applies to the other two. The tooth is very elongate, narrow anteriorly, with an elongate, flat but not procumbent anterior cingular shelf which is inclined lingually at about 45°. The metalophid is sharp, almost straight, and flat across the top. The hypolophid is slightly V-shaped with its concavity anterior and with the midpoint lower than either of the cusps. The protoconid has anterior and posterior crests. The anterior crest descends with progressively increasing steepness anteriorly, flattens out suddenly, and goes forth and joins the anterior cingular ridge. The cingular ridge curves antero-lingually then postero-lingually and dies out anterior to, and slightly labial to the metaconid. It is separated from the metaconid by a short, straight antero-medially-directed valley which extends from the center of the base of the anterior side of the protolophid to the antero-labial corner of the tooth. In PM 4586 the antero-labial corner of the protoconid is sharply angled from its apex to its base rather than being rounded as in the complete tooth. The metaconid has sharp anterior and posterior crests. The anterior one flexes slightly as it descends the cusp, and ends in a small cuspule located postero-lingual to the opening of the cingular valley. The posterior crest of the metaconid is straight, extends from the apex of that cusp to near the transverse valley, and swings labially as it disappears.

The entoconid has an anterior crest which is continuous with the hypolophid. The crest descends the front edge of the cusp, swings labially, and dies out before reaching the central valley. This crest and the posterior one of the metalophid leave an open symmetrical U-shaped notch.

The midlink is a low but sharp crest that extends postero-labially, then postero-lingually, from the apex of the protoconid. It descends the posterior face of the protoconid to the median valley, where it

turns slightly labially and climbs the anterior face of the hypoconid. It disappears about half-way up that cusp. In PM 4483 the midlink appears to have joined the hypoconid at its apex.

The hypoconid has an anterior crest which extends antero-labially. The crest is labial to the midlink, which it does not join. The crest dies out about half-way to the base of the cusp.

When viewed from the labial side, the metaconid and entoconid have a columnar appearance rather than a tapered one because of the crests.

These specimens resemble the lower molars and dP_4 of *Dorcopsis* and *Thylogale* in having crests on the cusps. The dP_4 of *Dorcopsis* has the protoconid and metaconid fused, and thus lacks a protolophid. In *Wallabia eugenii* the dP_4 and all lower molars have a protolophid, but the cresting is less developed. In *W. parryi* the dP_4 also has a protolophid, but the crests on the metaconid and entoconid are joined to form a lingual link. The Hamilton specimens are most like *Thylogale billiardieri* in having a protolophid, a similarly tapered procingulum with the antero-lingual valley, and crested cusps. However, the posterior end of the dP_4 of *T. billiardieri* is flatter than that of the Hamilton specimens.

The M_1 (PM 4564, Pl. XXIII, Figs. B–E) is elongate, but not narrowed anteriorly. It has a large procumbent procingulum and the metalophid is rounded and nearly level, with a small notch at its midpoint. The hypolophid is broadly V-shaped and is slightly depressed at its midpoint. The anterior crest of the protoconid arises below the apex of the cusp, runs antero-lingually, then anteriorly and joins the procingulum. Lingual to the forelink is a broad, flat, cingular shelf that is inclined posteriorly at about 20°. The cingulum itself extends lingually and postero-lingually but does not join the metaconid. Labial to the forelink there is a narrow cingular shelf which extends from the anterior end of the tooth, in a rootward and posterior direction, to the base of the protoconid. The outer edge of this shelf does not merge directly with the protoconid. Instead, it is notched and then expanded into a cingular bulge on the antero-labial and labial sides of the protoconid. The metaconid has an anterior crest which extends rootward and labially and disappears abruptly at about two-thirds of the distance to the base of the cusp. The protoconid and metaconid lack posterior crests.

The entoconid and hypoconid have weak anterior crests. The midlink arises near the apex of the hypoconid, extends anteriorly and

lingually, then turns anteriroly and joins the metalophid labial to the midline of the tooth. At its lowest point the midlink rises about halfway from the base of the tooth to the crests of the lophs. There is a small transverse spur near the low point on the midlink. There is a small, low, horizontal postcingular ridge. The enamel is smooth.

The two M_2s that show wear (PM 4576, Pl. XXIV, Figs. A–D; NMV-P26420) are so much alike that a single description will serve for both. They are relatively broad and rectangular in outline. The metalophid and hypolophid of both teeth are gently curved. The procingulum is large, procumbent, and rounded in outline and is separated from the metaconid as in the M_1. The forelink arises at the apex of the protoconid. In NMV-P26420 it extends in a nearly straight line antero-lingually and joins the anterior edge of the cingulum. In PM 4576 the forelink extends antero-lingually, then anteriorly and joins the cingulum. The position of the forelinks of both teeth is located closer to the midline of the tooth than in the M_1. Hence, the labial cingular shelf is larger than in the M_1, and the labial cingulum bulges. The lingual portion of the anterior cingular shelf is flat and is inclined posteriorly at about 20° as in the M_1. The midlinks of the two teeth differ from one another in the same way as the forelinks, that of NMV-P26420 being nearly straight and that of PM 4576 being bent lingually first, then running forward to the metalophid. The metaconid and entoconid have weak anterior crests which disappear about one-third of the way down the cusps. NMV-P26420 has a very small postcingular ridge as in the M_1, while PM 4576 has only a weak bulge in that region.

The two fragmentary posterior molars (PM 4451 and PM 4432, Pl. XXIV, Figs. E, F) consist of the anterior half of a tooth in the latter and the antero-lingual quarter of a tooth in PM 4451. The metalophids of both are curved and in PM 4432 the crest is wavy. The forelink is continuous with the metalophid and extends in a sigmoid curve antero-lingually then anteriorly, and joins the anterior edge of the tooth. The forelink is located close to the labial side of the tooth, and the labial cingular shelf is much reduced from the condition in the M_2s discussed above. The procingulum is procumbent and broad, and the cingular shelf is flat and inclined posteriorly as in the other lower molars. It does not reach the metaconid. The metaconid has a rounded anterior crest which gradually fades out halfway down the cusp. The junction of the midlink with the metalophid is located slightly labial to the midline of the tooth, and rises only about one-third of the distance up the back of the lophid.

Measurements.—See Table 6.

TABLE 6.—Dimensions of the Hamilton teeth assigned to *Thylogale* sp. indet. and of a Recent specimen of *T. billiardieri* for comparison (in millimeters)

		Occlusal length (outer surface)	Anterior crown height	Posterior crown height
Left I^2	(PM 4733)	4.1	6.4	5.2
Right I^3	(PM 4731)	4.8 (to notch)	—	—

		Length, tip to enamel line (labial side)	Maximum width
Left $I_{\bar{1}}$	(NMV-P26419)	16.2	6.4
Left $I_{\bar{1}}$	(FM 81526)	— (not exposed)	6.6

		Length	Anterior width	Posterior width
M^2	(PM 16802)	6.8	5.2	4.6
M^2	(NMV-P26421)	—	—	4.5
$dP_{\bar{4}}$	(PM 4438)	4.5	2.1	2.8
$dP_{\bar{4}}$	(PM 4483)	—	—	2.8
$M_{\bar{1}}$	(PM 4564)	5.6	3.0	3.3
$M_{\bar{2}}$	(PM 4576)	6.1	4.0	4.1
$M_{\bar{2}}$	(NMV-P26420)	5.8	3.9	4.0
$M_{\bar{3}}$ or $M_{\bar{4}}$	(PM 4432)	—	4.8	—

Discussion.—We believe that the materials referred to the genus *Thylogale* as *Thylogale* sp. indet., represent a single taxon which is new. As in the case of the *Dorcopsis* material, no formal name is being proposed because of some uncertainty regarding the association of some of the cheek teeth.

The closest resemblances of the Hamilton *Thylogale* materials among Recent species are to *Thylogale billiardieri,* but they share many features with other species of the genus and with those of *Dorcopsis.* The cheek teeth, especially the molars, of these two genera have many characters in common and consistent differences are few and subtle, particularly in the lower teeth. They appear to be as follows:

Upper cheek teeth of *Dorcopsis* are more nearly square than those of *Thylogale* which are more elongate.

The dP^4 of *Dorcopsis* has a parastyle which is larger relative to the size of the tooth than is that of *Thylogale.*

Forelinks are present in all upper molars of the living species of *Dorcopsis* and virtually absent in *Thyogale.*

The procingulae of the molars of *Dorcopsis* extend broadly across nearly the entire front edges of the upper teeth, while in *Thylogale* they occupy only the central part of the anterior edges of the teeth.

The $dP\frac{4}{4}$ of *Thylogale* has a definite metalophid, while that of *Dorcopsis* has a single laterally compressed cusp in this position.

The procingulae of all lower cheek teeth of *Thylogale* have flattened or only slightly basined occlusal surfaces which are not bounded lingually by a ridge, while in *Dorcopsis* they are basined and bounded by a lingual ridge.

The lower cheek teeth of *Dorcopsis* usually have stronger anterior crests on their lingual cusps than are found in those teeth in *Thylogale*, but wear may quickly obscure this difference.

Because so many dental characters in these genera show interspecies variation and variation within the tooth row, and because the size ranges of the various species overlap broadly, the identification of individual teeth is difficult. In an attempt to solve this problem, bivariate scatter diagrams have been made (*Appendix* Graphs F, G, H, I). These plot length *vs.* anterior width for the molariform teeth ($dP\frac{4}{4}$ through $M\frac{4}{4}$) for *D. mülleri*, *D. hageni*, *Dorcopsulus* sp. (probably *D. macleayi*), *Thylogale brunii*, *T. stigmatica*, and *T. billiardieri*. These scatter diagrams show the progressive changes in size and proportions of the teeth along the tooth row for the small samples available to us. For *T. stigmatica*, the largest species sample with nine individuals, the amount of variation and overlap gives a suggestion of what can be expected in these genera of wallabies. As a means of further broadening the comparison tooth measures of two other samples are also presented (eight individuals of *Dorcopsoides fossilis* (Woodburne, 1967) and eight of *Setonyx brachyurus* (lower teeth only).

These scatter diagrams very clearly show that in the living species of *Thylogale* and *Dorcopsis* (and *Dorcopsulus* sp.), there is a progressive increase in the length of the molar teeth from $M\frac{1}{1}$ to $M\frac{3}{3}$. In *D. hageni* the $M\frac{3}{3}$ may be about equal to $M\frac{2}{2}$. A similar, but somewhat less marked, increase in anterior widths also extends back to $M\frac{3}{3}$ in the three genera. In *Thylogale* these trends continue to $M\frac{4}{4}$, but in *Dorcopsis* only the width measurements show increase of $M\frac{4}{4}$ over $M\frac{3}{3}$. In *Setonyx brachyurus* $M\frac{4}{4}$ is shorter than $M\frac{3}{3}$, and widths are equal. In the rear of the upper molar series the trend changes: M^3 and M^4 are nearly the same size in *Thylogale*. The one *Dorcopsis* available having M^4, has that tooth somewhat longer and decidedly narrower than its M^3.

Placement of the measurements of the Hamilton specimens on these scatter diagrams provides no clearcut indication of their affinities. However, it does give us one more means of comparison by which we can both 1) assess the reasonableness of the assignments that were based in part upon other criteria, and 2) gain a better idea of the dentitions they represent.

Looking first at the upper molariform teeth, we see that the three which we have assigned to *Dorcopsis* sp. (PM 4433, PM 4434, NMV-P26417) plot to form a cluster that can be interpreted in different ways. The cluster is tight enough that the specimens all could be examples of the same tooth, but at the same time it is open enough, and intermediate enough, that they could also represent either the dP^4 or M^1 of a species close to *D. mülleri* or *D. hageni*. Tedford (personal communication, 1968) has suggested that PM 4433 may be a dP^4 or M^1, but we consider that the great breadth of the procingulum makes the dP^4 interpretation quite unlikely. We therefore consider this tooth and PM 4434 (for the same reason) to be molars, probably M^1s. NMV-P26417 with its broad, but tightly-appressed (i.e., not procumbent) procingulum, appears to be one of the more posterior molars, yet its length and width proportions fit an M^1 interpretation best. One other possible interpretation is that these teeth may be the M^3 or M^4 of a form near *Dorcopsulus*. As a *Dorcopsis* near *D. mülleri* or *D. hageni*, the Hamilton species would be characterized by having relatively narrow upper molars, but if its ties should be with *Dorcopsulus*, then they would be characterized by having more elongate proportions. Whatever the case, they are somewhat intermediate in terms of proportions. The one complete upper molar referred by us to *Thylogale* sp. as probably M^2, M^3, or M^4 (PM 16802) compares quite well in its length–width proportions with the M^4 of *T. stigmatica*. Unfortunately, the M^4 of *T. billiardieri* is unknown to us, but if the trends seen in the pattern of proportion changes along the tooth row follow those of the other species, PM 16802 should compare equally well with it, too. In fact, the comparison is reasonably good with the M^3 in those species.

Turning to the lower teeth, it may be seen that the only complete Hamilton specimen which we have assigned to *Dorcopsis* sp. (PM 4565) is shorter than the others (PM 4564, NMV-P26420, PM 4576) which are identified as *Thylogale* sp., and in size, proportions, and morphology it is closest to the M_2 of *D. mulleri*. The three *Thylogale* molars and the dP_4 (PM 4438) are all proportioned so that they

combine to make a pattern that is most reasonably interpreted as that of a species near to *T. billiardieri.*

The morphology of PM 4438 and PM 4564 indicates that both are teeth belonging to the anterior portion of a cheek tooth series, but the presence of a distinct metalophid on PM 4438 appears to rule out any possibility of its being the $dP_{\overline{4}}$ of a *Dorcopsis,* in which genus this lophid is not developed. It could well be referred to *Thylogale,* however, because in the species of that genus the $dP_{\overline{4}}$ not only has a definite metalophid, but has a broad and well-developed one. The relatively very long and narrow proportions of PM 4564 and its labially open, flat-bottomed procingulum make it hard to consider it to be anything other than the $M_{\overline{1}}$ of a species of *Thylogale.* The $dP_{\overline{4}}$ or $M_{\overline{1}}$ of *Dorcopsis* both have a more rounded valley floor that is cut off (without a lingual exit) by a ridge.

The other two teeth (NMV-P26420 and PM 4576) are of a size and proportion that fits with either the $M_{\overline{2}}$ (or possibly $M_{\overline{3}}$) of a *Thylogale,* or the $M_{\overline{1}}$ or $M_{\overline{2}}$ of a *Dorcopsis,* but their weak cresting fits the *Thylogale* pattern better than that of *Dorcopsis.*

Thus the morphology and size of all of the complete lower molariform teeth, except PM 4565, appear to be consistent with their belonging to one taxon, and that to be a species of the genus *Thylogale.*

The Hamilton *Thylogale* material resembles *T. billiardieri* in a large number of characters such as general size, structure of the upper and lower incisors (so far as they are known), and the structure of the $P_{\overline{3}}$. It shows some differences which indicate that it is not assignable to that species. They are: the labial inclination of the procingulum shelf of $dP_{\overline{4}}$, the lesser development in breadth of the metalophid of the $dP_{\overline{4}}$, the slightly larger (absolutely, but not relatively) size of the molars, and the relatively broader upper procingulae, which are somewhat intermediate in their development between those in the extant species of *Dorcopsis* and *Thylogale.*

Macropodinae *incertae sedis*

There are a number of isolated macropodine teeth and fragments of teeth which cannot be identified at present. They fall roughly into two size groups, large and small. The large represent animals in the *Macropus* size range and the small are from animals in the wallaby size range. They are grouped on this basis for description, but this does not imply close taxonomic affinity.

Large-sized macropodines

Material.—A complete, nearly unworn left molariform tooth, probably a dP^4 (PM 4429, Pl. XXVIII, Figs. A–E); antero-lingual corner, worn right upper molar (PM 4498, Pl. XXVIII, Fig. F); antero-lingual corner, worn left lower molar (PM 4441); posterior half of a slightly worn right lower molar (NMV-P26422); posterior edge of a lower molar showing wear facet of hypolophid and a large interdental facet (PM 4469); two insignificant molar fragments (PM 4435; PM 4732), and the postero-lingual corner of a very worn hypolophid (PM 4715).

Description.—The complete upper molar or dP^4 (PM 4429) is somewhat larger and lower crowned than the upper molars of *Wallabia agilis* but is relatively wider. It is similar in proportion to those of *W. bicolor,* but is lower crowned. The protoloph and metaloph are curved. The paracone and metacone have distinct, sharp labial ridges on the anterior and posterior sides. The anterior ridge of the paracone joins the labial edge of the procingulum. The posterior ridge of the paracone extends in a broad curve to the base of the cusp where it branches. The lingual branch quickly dies out and the labial one meets but does not join an independent short spur on the base of the metacone. The anterior ridge of the metacone curves lingually toward the base of the cusp and dies out before reaching the central valley. Several genera of Recent macropodines have upper molars with these labial crests or ridges (*W. bicolor, Setonyx brachyurus, Thylogale, Dorcopsis*) and at least three extinct forms do also (*Sthenurus tindalei* (Tedford, 1966), and the *Dorcopsis* and *Thylogale* in this fauna), but none shows quite the development of the condition as presented by PM 4429. Upper molars of the extinct *Protemnodon* have these ridges reduced and *Prionotemnus* lacks them (Stirton, 1955).

The midlink is joined to the apex of the protocone. It extends in a straight line postero-labially to the center of the tooth, then turns posteriorly and joins the metaloph. It does not reach the crest of the metaloph. The highly crested part of the midlink is about equally formed by the protoconal spur and the basal anterior metaloph spur as in *Setonyx, Dorcopsis, Dendrolagus,* and *Lagorchestes.* In the central valley the midlink has a lingually-directed kink. The labial concavity in the midlink formed by this kink is filled by a small pillar. The midlink and the postero-labial crest of the paracone form a basin in the central part of the tooth between the cross lophs. Such a basin is a feature of the dP^4 of *Protemnodon* and is found in upper molars of *W. bicolor, Setonyx, Dorcopsis, Thylogale billiardieri, Den-*

drolagus, and *Petrogale*, but in these species the labial border of the basin is formed by the labial crests of the paracone and metacone and is often incomplete.

The procingulum is slightly basined. The anterior edge is connected labially to an anterior crest of the paracone. The widest part of the cingulum is located near its lingual end. The anterior border joins the protocone before reaching the lingual edge of the tooth. There is only a trace of a forelink.

A small postlink extends rootward and labially from the hypocone, becomes horizontal across the base of the tooth and ends at the base of the metacone. It forms a small pit-like cingular basin. A short ridge extends rootward on the back of the metacone but does not quite reach the postlink.

The tooth shows the beginning of wear. There is a small transversely elongated interdental facet on the middle of the anterior edge of the procingulum. There is another equal-sized abrasion facet adjacent to this on the occlusal surface of the anterior edge of the procingulum. The crest of the protoloph has a slightly oblique (nearly vertical) facet on its anterior edge. The metaloph shows no sign of wear.

This complete upper tooth has many resemblances to the upper molars of *Dorcopsis*, *Dendrolagus*, *W. bicolor*, and *Thylogale billiardieri*. It differs from all of them in its much greater size and in the combination of characters, many of which are found in one or more of the Recent species. The best comparisons are with the dP^{4} of *Protemnodon brehus* (Tedford 1967, fig. 25B, table 36) and *Protemnodon* sp. (Stirton 1963, fig. 6A and p. 120) in terms of form and proportions as well as size. The dP^{4} of *Protemnodon* is very molariform as is the Hamilton specimen, and these close resemblances suggest that PM 4424 is probably a dP^{4} of a species of *Protemnodon*.

Measurements.—The measurements in millimeters for PM 4429 are: length 11.3, anterior width 10.1, posterior width 10.6.

Description.—The half lower molar (NMV-P26422) has a hypolophid that is as large as that of the lower molars of *Macropus* or *Protemnodon*. In crown view it is broadly curved and lowest in the center, and lacks the strong root to crest taper that is characteristic of *Macropus*. The midlink arises just below the apex of the hypoconid and is not confluent with the hypolophid. The portion of the midlink that is preserved extends rootward and changes its direction along a gentle curve from antero-labially to anteriorly at its broken

edge. There is a very faint, gently rounded ridge that extends from the entoconid antero-lingually to the broken edge of the tooth. It is confluent with the hypolophid, but does not join the midlink. There is a prominent rounded bulge in the position of the postcingulum.

This tooth differs from the lower molars of *Macropus* and *Wallabia* in lacking the strong lateral taper toward the crest of the lophid in unworn teeth and in the confluence of a strong midlink and the hypolophid. It is as large as that in some species of *Protemnodon*, but differs in having a slightly more curved hypolophid. It is very similar in size (posterior width 8.5 mm.) and general appearance to the lower molars figured by Bartholomai (1967) and referred by him to *Troposodon minor*. Features responsible for the similarity of appearance are: the degree of curvature of the hypolophid, the height and curvature of the midlink, and the presence on the anterior face of the hypolophid of a faint accessory ridge which ends close to, but not joined to the midlink. This last character is apparently better developed in *Troposodon* than in the Hamilton tooth. No ornamented shelf is formed in the median valley of the latter.

The remaining fragmentary large macropodine teeth convey only scant information. The worn right upper molar (PM 4498) consists of the antero-lingual corner of a tooth that is about the same size as PM 4429. It may have been slightly more massive and higher crowned when unworn than the complete tooth (Pl. XXVIII, Fig. F). In the worn left lower molar (PM 4441) the enamel of the metaconid has been breached, and its procingulum forms a transverse "lophid" which is connected to the protolophid by a low broad forelink.

Discussion.—The large indeterminate macropodine material probably represents two taxa. One, represented by the large upper molariform tooth (PM 4429), has many dental resemblances to upper molars of *Dorcopsis* and *Dendrolagus*, but shows much more similarity to the dP^4 of *Protemnodon*. Its affinities probably lie with that genus. The other, represented by the hypolophid of a large lower molar (NMV-P26422), has many characters in common with the extinct genera *Protemnodon* and *Troposodon*.

It is doubtful that these two large teeth could represent the same taxon. In general, upper molariform teeth that have the kind of cresting seen in PM 4429 should be accompanied by lower molars with stronger cresting on the labial cuspids than is seen in NMV-P26422.

Small-sized macropodines

Material and descriptions.—This category consists of wallaby tooth fragments identifiable only to the subfamily level. They are simply listed here with a few brief comments given in some cases. Several are illustrated.

PM 4559—anterior edge of a small, very highly crested, narrow premolar blade somewhat like that of the $P_{\overline{3}}$ of *Dorcopsis mülleri* (AMNH 108044), and in other ways like that of the deeply clefted blade of *Thylogale brunii* (PM 31864), (Pl. VI, Fig. A).

PM 4558—posterior half of a small, high crested, serrate premolar blade. This could be the back half of PM 4559, but there is no good contact. If such were the case, a tooth quite like the $P_{\overline{3}}$ of the mentioned *D. mulleri* would result, but it would be smaller.

PM 4583—posterior edge of a hypolophid of a small wallaby, possibly *Thylogale.*

PM 4734—fragment of a lateral upper incisor.

PM 4578—piece of a lower incisor blade, possibly *Thylogale.*

PM 4448—a worn ?protocone, possibly referable to *Thylogale.*

PM 4593—posterior end of a premolar blade similar to the $P_{\overline{3}}$ or $P_{\overline{4}}$ of *Dorcopsis* and *Thylogale,* but not exactly comparable (Pl. XXIX, Fig. A).

Family Diprotodontidae

Palorchestes Owen, 1874

Palorchestes cf. **painei** Woodburne, 1967

Material.—A left lower molar, probably $M_{\overline{1}}$ or $M_{\overline{2}}$ (PM 16801, Pl. XXX).

Description.—The tooth is elongate, rounded in front, and rounded but somewhat flattened in back. It is weakly but noticeably constricted in the middle when viewed in the occlusal aspect. The crown is relatively low: the ratio of protolophid height to tooth length is 0.65. Comparative values of 0.74 or 0.73 were found for a slightly worn $M_{\overline{2}}$ and an unworn $M_{\overline{3}}$ (?), respectively, for some Wellington specimens of *P. azael* (PM 1580; PM 1665). The more worn $M_{\overline{1}}$s in the Wellington specimens gave values of 0.68 and 0.60. The crests of the lophids are concave forward and they cross the tooth somewhat diagonally; the labial edge is more anterior than the lingual. The lingual sides of the lophids rise almost straight up from the tooth

base, but they are not flattened in this plane as is often the case with those of *P. azael.* The labial sides of the lophids are rounded, and they do not stand quite as straight up as the lingual sides. There is a massive, rugose, weakly crested anterior ridge that runs from the apex of the protoconid down to the level of the cingulum. The procingulum bulges up rapidly on the labial side of the front edge of the tooth to meet this ridge, and continues in a lingual direction, gradually approaching the crown base. The junction of the "forelink" ridge from the protoconid with the cingulum is weak and the cingulum protrudes slightly where it crosses in front of the ridge. Thus, the two structures do not merge fully.

The protolophid shows the faint beginning of wear across its entire width in a facet inclined at about 45° up from the occlusal plane of the tooth. The hypolophid is narrower apically than the protolophid and its ridge turns smoothly forward as it crosses the hypoconid. The ridge then swings diagonally, forward, and lingually, so as to descend into the transverse valley as a stout midlink. It joins a much weaker, straight, rapidly descending ridge from the protolophid above the midpoint of the floor of the valley. The disproportionately small contribution of this protolophid part of the midlink to the whole is a notable feature of the tooth. The postlink, which is characteristic for the diprotodonts, is well developed and joints a stout postcingulum. The postlink begins as a faint ridge that runs down from the middle of the hypolophid to the level of the cingulum where it rapidly enlarges as it levels out and swings backward to meet the cingulum. The cingulum rises rapidly from each side toward this junction. The postcingulum is perhaps a little less well developed than in *P. azael.*

Measurements.—See Table 7.

Discussion.—The smaller size, relatively low crown height and somewhat weaker links and pro- and postcingulae suggest a primitiveness for this specimen in comparison with *P. azael* and indicate a close relationship to *P. parvus* and *P. painei.* The Hamilton specimen is only slightly larger than the largest $M_{\bar{1}}$ of *P. painei* reported by Woodburne (1967). It also resembles the $M_{\bar{1}}$ of *P. painei* in the lack of a well-developed labial cingulum. The transverse valley has an open V-shaped profile when viewed from the labial side.

The calculation of ratios of protolophid height/tooth length for *P. painei* from Woodburne's (1967) data is impossible for $M_{\bar{1}}$ and $M_{\bar{2}}$, and not entirely satisfactory for $M_{\bar{3}}$ and $M_{\bar{4}}$, but the results suggest

TABLE 7.—Measurements in millimeters (length × anterior width) of the lower molar tooth of *Palorchestes* sp. indet. (PM 16801) from the Hamilton fauna compared with those of two specimens of *P. azael*, Owen from the Wellington Caves in the Field Museum collection, and with those of *P. parvus* (data from Woods, 1958). Additional comparisons may be seen in *Appendix* Graph J, where these data are plotted along with those given by Woods for *P. azael*, the best-known species of the genus, and by Woodburne (1967) for *P. painei*.

	$M_{\bar{1}}$	$M_{\bar{2}}$	$M_{\bar{3}}$	$M_{\bar{4}}$
The Hamilton *Palorchestes* sp. indet. (PM 16801),	17.1 x 11.0	—	—	—
P. parvus DeVis (from Woods, 1958)				
(F. 783 - Type)	19.7 x 12.3	20.6 x 12.6	20.8 x 12.8	20.6 x 13.1
(F. 786)	—	20.8 x 13.7	21.1 x 14.1	22.0 x —
(F. 793)	—	19.2 x 11.1	21.0 x 12.3	20.0 x 12.4
(F. 2969)	—	—	21.0 x 14.6	21.0 x 13.9
(F. 3300)	—	19.1 x 11.8	19.8 x —	19.1 x 12.2
(F. 3301)	—	—	19.4 x 12.1	—
P. azael from Wellington				
(PM 1580)	23.9 x 14.5	25.8 x 15.8	—	—
(PM 1665)	21.4 x 12.1	—	24.1 x 14.4	—

a maximum expected value of about .52. This is somewhat lower than the value of .65 for the Hamilton specimen.

Infraclass Eutheria

Order Chiroptera

Suborder Microchiroptera

Incertae sedis at all lower taxonomic levels

Material.—One left lower molar in a mandibular fragment (PM 4458, Pl. XXIX, Fig. H).

Description.—This specimen is the only representative of the placental mammals known from the Hamilton fauna. It was mistakenly considered to be a phascogaline in our earlier report (Turnbull et al., 1965) but our detailed comparisons indicate chiropteran affinities. The molar is probably an $M_{\overline{2}}$ or $M_{\overline{3}}$ and is about the size of these teeth in the living *Tadarida* (*Nyctinomus*) *australis* or *Nyctophilus goeffroyi*. Its length is 1.41 mm.; anterior width, 0.82 mm.; and posterior width, 0.80 mm.

The trigonid is higher than the talonid, but not as much higher as it is in the phascogalines. The three cusps of the trigonid form a triangle in which the paraconid and metaconid are closer to each other than either is to the protoconid. The profiles of the ridges from protoconid to paraconid, and from protoconid to metaconid are V-shaped, but lack the deep narrow clefts seen in the teeth of phascogalines. The three cusps of the trigonid are not as high above the trigonid basin (because basin is high relative to crown base) as are those of the phascogalines.

The talonid basin is bounded lingually by a blade-like ridge that connects the entoconid with the metaconid. The entoconid is relatively larger than in the lower molars of the phascogalines. There is a well-developed hypoconid, and a small but distinct hypoconulid which lies close to the entoconid at its base. Talonid and trigonid are very close to the same size. There is a well-developed and continuous cingulum on the anterior, labial, and posterior sides of the tooth. In this it contrasts with the phascogalines, in which the cingulum is reduced labially.

Dental features such as those mentioned in the preceding paragraphs serve adequately to eliminate the Phascogalinae from consideration, and to affirm the microchiropteran affinities of the specimen. However, within the Microchiroptera we've not been able to

determine with any certainty which of several families of the suborder the specimen belongs to. We suspect that there are too many genera in which the lower molars have the same basic form, for an identification based upon a single lower tooth to be clearcut. The two mentioned species, *Tadarida* (*Nyctinomus*) *australis* and *Nyctophilus goeffroyi*, both have lower molars that are very similar, and they are classified into two different families, Molossidae and Vespertilionidae (Nyctophilinae), respectively. Also several other genera of vespertilines (*Myotis, Pipistrellus, Eptesicus, Nycticeus,* and *Chalinolobus*) all have lower molars with a morphology that is very similar to one another and to the Hamilton tooth. (Specimens of *Myotis* and *Pipistrellus* available for comparison all have the hypoconulid either too well developed or too set apart from the entoconid. This would appear to rule out those genera, but the sample is too small to be certain of this.) The latter three vespertiline genera at least, and one other genus, *Hipposideros*—this from yet another family (Hipposideridae), also have lower molars with this same basic morphology. Thus, we concluded that we cannot make a family assignment for the Hamilton specimen.

Class indeterminate, probably Mammalia

Incertae sedis at all lower taxonomic levels

Material.—Five enamel caps (NMV-P26425, PM 4468, PM 4466, PM 4465, and PM 4599, Pl. XXXI, Figs. A–F).

Descriptions.—Four of the five specimens consist of what appear to be complete enamel caps. The fifth specimen is incomplete and has been sectioned to allow an examination of the structure of the enamel.

The teeth consist of elliptical enamel caps each with a closed central basin. The basins are shallow with smooth rounded bottoms. They fall reasonably well into three groups on the basis of size and morphology. The two middle-sized specimens (NMV-P26425 and PM 4465) each have a predominant, low, rounded cusp on one end. They have a variable number of smaller low cusps on the rim that borders the central basin. The smallest of the complete teeth (PM 4466) has its sole cusp on one end and has a smooth rim. One of the two middle-sized ones (NMV-P26425) has a relatively large cusp on each end, the larger of which appears to have had the enamel breached by wear at the apex.

The largest tooth of the four (PM 4468) has no bulbous cusps at its ends, but has a higher pointed one at one end and a number of small cusps on the rim of the central basin.

None of the teeth shows any sign of an interdental facet which would give some indication of the orientation in the jaw. No indication of the orientation can be obtained from what appears to be wear on one of the medium-sized teeth (NWM-P26425).

The sections of the incomplete tooth show an enamel structure which appears to be most like that seen in mammals. There are elongated enamel prisms to be seen in the transverse tooth section, oriented so that their full length is exposed. In the tangential tooth section one area on the extreme left side shows others similarly cut, but most of the section shows the prisms cut across nearly perpendicular to their axes.

The enamel prisms are relatively small; prism diameter being of the order of 3 to 5 micra. Most prisms are moderately twisted along the long axis, and there is a slight tendency for them to intertwine weakly. The twisting is most pronounced near the base (i.e., near the dentine-enamel boundary). In this respect the prism histology conforms to that of the relatively uncomplicated, untwisted pattern as is shown by Peyer (1968, Pls. 77A, B) for a mole and a bat. This would indicate, according to Peyer's interpretation, a relatively primitive type of mammalian enamel. In cross-section the prisms show much the same appearance as those of *Homo* as figured by Keil (1966, Fig. 51) or Lehner and Plenk (1936, Fig. 42). However, there seems to be a poorer alignment than is seen in the first of these examples.

None of the lower vertebrates shows a comparable enamel structure. Prismatic enamel is known for reptiles and amphibians, but in them it is not nearly as highly organized as in the mammals. Within the fishes, enamel occurs in crossopterygians and lungfish, but it does not have a prismatic structure. In some holosteans and in teleosteans enamel occurs as a collar or ring surrounding the tooth crown without forming the tip of the crown which consists of a highly specialized kind of dentine.

The combination of gross morphology and enamel structure indicates that the five enamel caps are most probably mammalian teeth, but any assignment to a lower taxonomic group would be purely conjectural at this time. They look most like teeth of microcleptids, some bats, or some small phalangerids with very atrophied last molars. They bear very little resemblance to the true teeth of *Ornitho-*

rhynchus. The teeth of the latter are multicuspate with ridges breaking the teeth up into two or more basins. Recognition of their affinities must await the discovery of additional, and probably more complete material.

Miscellaneous Scraps and Fragments

This category consists of the final residue of tooth fragments. Most of them are probably too fragmentary ever to be identified, but some show morphological features which may make them interpretable at some future date. Several hundred smaller chips with no structural features (grouped under PM 4597 and PM 4598) are not considered. The listed materials carry comments as to our tentative identifications.

PM 4595—a conical chip bearing four longitudinal ridges (Pl. XXIX, Fig. D).

PM 4560 and NMV-P26424—pieces from the center of a high serrate premolar blade (Pl. XXIX, Figs. E, G), possibly of a potoroine or macropodine.

PM 4730—two cusps, presumably the anterior-most ones of a minute premolar blade, possibly a potoroine (Pl. XXIX, Fig. C).

PM 4740—fragment that seems to have been a posterior end of a premolar blade, badly worn and with a good interdental facet.

PM 4447—indeterminate mammal tooth fragment.

PM 4491—indeterminate mammal tooth fragment.

PM 4494—indeterminate mammal tooth fragment.

PM 4497—indeterminate mammal tooth fragment.

PM 4577—indeterminate mammal tooth fragment.

PM 4580—indeterminate mammal tooth fragment (Pl. XXVII, Fig. C).

PM 4581—upper incisor, possibly potoroine or macropodine.

PM 4582—very worn tooth, possibly macropodid molar (Pl. XXIX, Fig. B).

PM 4714—fragment of a lower incisor, possibly macropodid or phalangerid.

PM 4716—indeterminate molar fragment, probably pseudocheirine.

PM 4736—fragment from the center of a premolar blade, possibly potoroine.

PM 4737—indeterminate tooth fragment, probably macropodid.

PM 4738—indeterminate mammal tooth fragment.

PM 4739—indeterminate mammal tooth fragment.

PM 4741—indeterminate mammal tooth fragment.

PM 4742—indeterminate mammal tooth fragment, probably macropodid.

PM 4760A–C—indeterminate mammal tooth fragment.

PM 4450—complete toebone, well preserved, probably mammalian.

PM 4743—scrap of bone, well preserved.

PM 4744—scrap of bone, well preserved, possibly fish.

PM 4757—indeterminate small mammal, proximal end ulna.

INTERPRETATION OF THE HAMILTON FAUNA

Faunal Composition

The Hamilton fauna as presently known is composed almost entirely of teeth and fragments of teeth belonging to the Mammalia. Bone is rarely preserved in the sediment containing the fauna and light skeletons would not be likely to preserve. This accounts for most of the lack of lower vertebrates since many have light, fragile skeletons. The lack of resistant structures, such as teeth of fish and reptiles, is probably either an indication that the wrong niches are being sampled, or that their structures are less resistant than thought. The absence of larger reptiles, such as varanids, is probably an accident of sampling.

Despite the presence of a considerable number of taxa (18) showing a moderate ecological breadth, there remain several obvious deficiencies in the representation of the faunal elements. Large-sized species are very poorly represented or are absent, and dasyurids and rodents are totally lacking. The dasyurid absence is surely an accident of sampling. Table 8 shows that a small number of individuals (43) could account for the materials collected to date. Thylacoleonids, dasyurids, and large herbivores probably had smaller population sizes than did the small herbivores, and they would be more likely to be missed in small samples.

It is also possible, but more difficult, to attribute rodent absence to an accident of sampling. Whenever comparable collecting techniques have been used on Pleistocene sediments in Australia and on Pleistocene or Tertiary sediments on other continents, rodent remains are almost always present if small-sized animal remains are found. In addition, rodents make up 37–53 per cent of the taxa of small mammals of Pleistocene faunas from Western Australian caves and 83–91 per cent of the individuals of those faunas where such data are known (Lundelius, 1960). The comparable figures for the small dasyurids are 27–29 per cent and 6–11 per cent, respectively. Thus, even allowing for considerable environmental differences between the

TABLE 8.—Composition of the Hamilton Fauna

Taxon no.	Class: Subclass: Order: Superfamily: Family: Subfamily: Genus and species	No. of specimens	Minimum no. of individuals
1	Mammalia: Metatheria: O. Marsupialia: Perameloidea: Parameliidae: Genus and species indet.	5	1
	Phalangeroidea: Phalangeridae: Phalangerinae:		
2	*Phalanger* cf. *gymnotis*	1	1
3	*Trichosurus* sp. indet.	3	2
–	?*Phalanger*, or ?*Trichosurus*, or genus indet.	5	2 or 3
–	*Incertae sedis*, near *Phalanger* or *Trichosurus*	5	1 or 2
4	*Incertae sedis*—genus and sp. indet. (minute)	2	2
	Phalangeroidea: Phalangeridae: Burramyinae:		
5	*Burramys* sp. indet.	4	2
	Phascolarctidae: Pseudocheirinae:		
6	*Pseudokoala erlita* n. genus and sp.	3	2
–	c.f. *Pseudokoala erlita*	4	1
7	*Pseudocheirus stirtoni* n. sp.	32	3
8	*Pseudocheirus marshalli* n. sp.	18	2 or 3
–	*Pseudocheirus* sp. indet.	14	4
	Macropodidae: Potoroinae:		
9	*Incertae sedis* near *Aepyprymnus*	1	1
10	*Incertae sedis* near *Hypsiprymnodon*	1	1
11	*Incertae sedis* near *Propleopus oscillans*	1	1
12	*Dorcopsis* sp. indet.	16	3 or 4
	Macropididae: Macropodinae:		
13	*Thylogale* sp. indet.	18	3 or 4
14	*Incertae sedis* (large form-A near *Protemnodon*)	2	1
15	*Incertae sedis* (large form-B)	3	2
—	*Incertae sedis* (?large A, or B, or ?)	3	?2
—	*Incertae sedis* (? *Dorcopsis* or *Thylogale*, or ?)	7	2 or 3
	Diprotodontidae: Palorchestinae:		
16	*Palorchestes* near *P. painei*	1	1
	Mammalia: Eutheria: O. Chiroptera: Microchiroptera:		
17	*Incertae sedis*, genus and sp. indet.	1	1
	?Mammalia: Subclass uncertain:		
18	*Incertae sedis* at all taxonomic levels	5	?1
TOTALS	18 mammalian species	155	43
	Miscellaneous scraps	27	6–8
		182	49

Western Australian caves with their probable owl pellet bias (see Schram and Turnbull, in press) and the deposit in the Hamilton area, it would be unlikely that the rodents would be missed by a sampling accident. The absence may be real, and this possibility deserves consideration.

If real, the absence of rodents can be interpreted in at least two ways. It is possible that at the time of accumulation of the Hamilton sample rodents were excluded from the particular environmental situation from which the fauna was drawn. This seems unlikely because rodents generally have representatives in most environments.

To date no rodents have been reported from pre-Pleistocene deposits in continental Australia, although one has recently been reported from Awe fauna of New Guinea (Plane, 1967). The Awe fauna has been dated radiometrically and is somewhat older than the Hamilton fauna. Although it is now certain that some rodents were in New Guinea by Late Pliocene time, it is possible that they had not entered continental Australia. The Torres Strait connection may not have been continuously available and their entrance into Australia may have been delayed. This would mean that the greater part, at least, of the Australian rodent radiation has taken place after Late Pliocene time (in 4.35 million years), rather than in post Late Miocene time (Simpson, 1961; Tate, 1951).

Comparisons with Other Faunas

Detailed comparisons of the Hamilton fauna with other fossil mammal faunas from Australia will be deferred until the material collected in 1966–67 is studied. However, because the Hamilton fauna has been dated radiometrically, and thus offers a key to the correlation of other Australian faunas with the Lyellian epochs, some preliminary comparisons are given here.

A comparison of the Hamilton *Dorcopsis* and *Palorchestes* material with Pleistocene representatives of these genera shows the Hamilton material to be clearly more primitive in both size and crown height. The Hamilton *Palorchestes* is distinctly smaller and lower crowned than *P. parvus* from the Chinchilla fauna of Queensland. The Chinchilla fauna has been considered to be Late Pliocene in age (Woods, 1956, 1960; Plane, 1967; Woodburne, 1967). Tedford (1966) questioned the age assignment of the Chinchilla to the Pliocene. His use of "later Pliocene or early Pleistocene" reflects this uncertainty. He has also pointed out that in southwestern Victoria, *P. parvus* lived well into the Pleistocene as evidenced by its occurrence in the

Strathdownie fissures. The more primitive condition of the Hamilton specimen also relates to the age assignment of the Chinchilla fauna. The radiometric date 4.35 x 10^6 years for the Hamilton fauna places it in the Late Pliocene (Evernden et al., 1964). At the present time it is uncertain as to whether the difference in the *Palorchestes* material indicates a younger age for the Chinchilla fauna, perhaps early Pleistocene, or an ecological difference.

The Hamilton *Palorchestes* is very similar to *P. painei* from the Alcoota fauna, and the Hamilton *Dorcopsis* is similar to the Alcoota *Dorcopsoides* in crown heights of the molars. Also, when sizes and proportions of the cheek teeth in these species are compared (*Appendix* Graphs G, I, J) it may be seen that the *Palorchestes* materials from the two faunas are nearly identical, while the Hamilton *Dorcopsis* shows somewhat greater differences from *Dorcopsoides*. These similarities suggest that the Hamilton and Alcoota faunas may be closer together in age than was originally thought (Woodburne, 1967; Stirton et al., 1968; and see also Stirton et al., 1961) and that the Alcoota fauna may be somewhat younger than late Miocene or early Pliocene.

The Hamilton fauna has been shown to be younger than the Awe fauna of New Guinea, but, unfortunately, there is very little in common taxonomically between the two faunas which would allow some evaluation of the amount of ecological control on persistence of more primitive types in the lower latitudes (Plane, 1967). A comparison of the Hamilton *Dorcopsis* with the Awe form is not particularly helpful, because of the size discrepancy between the two species and because the best Awe specimen is at a more advanced wear stage than are most of the Hamilton teeth.

Ecological Interpretation

Of the 18 mammalian taxa in the Hamilton fauna, four (*Dorcopsis* sp., *Phalanger* sp., the potoroine similar to *Hypsiprymnodon*, and the peramelid) are closely related to forms which today are found in wet sclerophyll or rain forest areas in northern Australia or New Guinea, or both (Tate, 1945a; 1948a; 1948b; Keast, 1961; Troughton, 1962; Marlow, 1962). The presence of three species that are either assignable to *Pseudocheirus*, or to a closely related genus (*Pseudokoala*), is also suggestive of a wet forest environment for the fauna. The only places today where more than two species of *Pseudocheirus* are found are wet forest areas in northern Queensland and New Guinea (Tate, 1945b). Three other taxa (*Thylogale* sp., *Burramys*

sp., and the *Cercartetus*-like phalanger) probably indicate forest conditions, too, although one species of the latter genus is now distributed through dry scrub forest (Wakefield, 1963). The remainder of the fauna is made up of forms whose Recent relatives are widely distributed in Australia or, in the case of the extinct forms, whose ecological requirements are unknown. At least one is related to a Recent species (*Aepyprymnus rufescens*) that is reported to inhabit open woodland (Marlow, 1957, 1958). It may indicate the presence of local open areas or it may have had ecological requirements different from the modern form. Thus the fauna appears to be a forest fauna, and apparently the forest was considerably more humid than those in Western Victoria today.

This conclusion thus reinforces the earlier one (Gill, 1957) regarding the general environment of the Hamilton area at the time of formation of the fossil soil with its fauna.

SUMMARY AND GENERAL CONCLUSIONS

The Hamilton fauna consisting of 18 mammalian taxa (mainly marsupial) has been collected from a fossil soil developed on the Kalimnan limestone of Pliocene age on the Grange Burn, four miles west of Hamilton, Victoria. The material consists almost entirely of teeth collected by wet sieving. The soil is overlain by a basaltic flow which has been radiometrically dated at 4.35 ± 0.1 MY. The presence of charred stumps under the basalt indicates contemporaneity of the fossils and the flow.

Large-sized species are either poorly represented or are absent, and lower vertebrates, dasyurids, and rodents are absent. With the exception of the rodents, these deficiencies in the fauna are believed to be the result of either destructive burial environment or of sampling accidents. The absence of rodents is believed to be real because of their abundance in Pleistocene deposits.

All taxa represented, except the bat and the five small enamel caps described on pages 70–72, fall into known Recent or Pleistocene marsupial subfamilies. Most are clearly related to known Recent or Pleistocene genera, although some may require generic separation when they become better known. Three new species and a new genus of pseudocheirines are named, and probably many of the unassigned and unnamed specimens of other families represent undescribed species, but the inadequacies of the materials militated against naming of new taxa. Only a few, such as *Burramys* and *Palorchestes*, show differences from Recent or Pleistocene relatives that might indicate primitiveness. The Hamilton *Burramys* sp. has characters of its $P\frac{4}{4}$s which could be regarded as primitive. The lower molar of *Palorchestes* is smaller and slightly more generalized than any of the teeth of the small Pliocene–Pleistocene species, *P. parvus* from Queensland, and is very similar to the ? Miocene–Pliocene Alcoota, *P. painei*. Taxa of the two best represented groups, Pseudocheirinae and Macropodidae, show no obvious indications that would mark them as being either more primitive or more advanced than the known fossil or Recent close relatives.

As a whole, the fauna appears to be a wet forest fauna with many indications that the environment was a wetter one than presently occurs in the Hamilton region. In composition, except for its lack of dasyurids and rodents, and in evolutionary grade with its strong similarities to Pleistocene and Recent faunas, it is about what one would expect of a Late Pliocene fauna. It thus supports broadly the late Tertiary faunal correlations that have been made during the past two decades, but it provides suggestive evidence that the Alcoota fauna may be slightly younger than has been thought.

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PLATES
AND
APPENDIX

PLATES

Plates I–XXXI are comprised almost entirely of steroscopic photopairs (The exceptions are figures D and E of Plate VII and figures E and F of Plate XXXI) illustrating all of the taxa of mammals in the Pliocene, Hamilton fauna from the Grange Burn. Most of the better specimens are shown. The marsupial families are covered as follows: Peramelidae—Pl. I; Phalangeridae—Pls. II–VI; Phascolarctidae—Pls. VII–XVIII; Macropodidae—Pls. XVIII–XXVIII; Diprotodontidae—Pls. XXX. The few non-marsupialian remains, and some miscellaneous materials are illustrated on Pls. XXVII, XXIX, XXXI.

Abbreviatons for major cusps are as follows: end=entoconid; esd=entostylid; hy=hypocone; hyd=hypoconid; hyld=hypoconulid; me=metacone; med=metaconid; mele=metaconule; mes=mesostyle; msd=metastylid; pa=paracone; pad=paraconid; pas=parastyle; pr=protocone; prd=protoconid; prle=protoconule.

PLATE I.—Peramelid teeth. Arrows mark certain other features discussed in the text. e = ridge connecting entoconid to the posterior ridge of metaconid. h = ridge connecting hypoconid to the back edge of trigonid. **A–D.** PM 4499. Trigonid of a right molar, lateral, crown, posterior, and medial views. Scale approx. × 13. **E–F.** NMV-P26406. Partial right trigonid, crown, and posterior views. Scale approx. × 15.

med
prd
pad
e
h
A
B
C
e
h
e
D
prd
med
h
pad
2 mm
E
F
prd
med
2 mm

PLATE II.—Teeth of various phalangerines. Scale approx. × 13. **A.** *Incertae sedis*, near *Phalanger* or *Trichosurus*, PM 4722, tip of left upper canine, crown, and lateral views. **B.** *Trichosurus* sp. indet., PM 4557, fragment of a left $P_{\overline{4}}$, crown view. **C.** *Phalanger* cf. *gymnotis*, PM 4457, a heavily ribbed left $P_{\overline{4}}$, lateral and crown views. **D.** *Trichosurus* sp. indet., PM 4556, fragment of an anterior edge of a left $P_{\overline{4}}$, crown view.

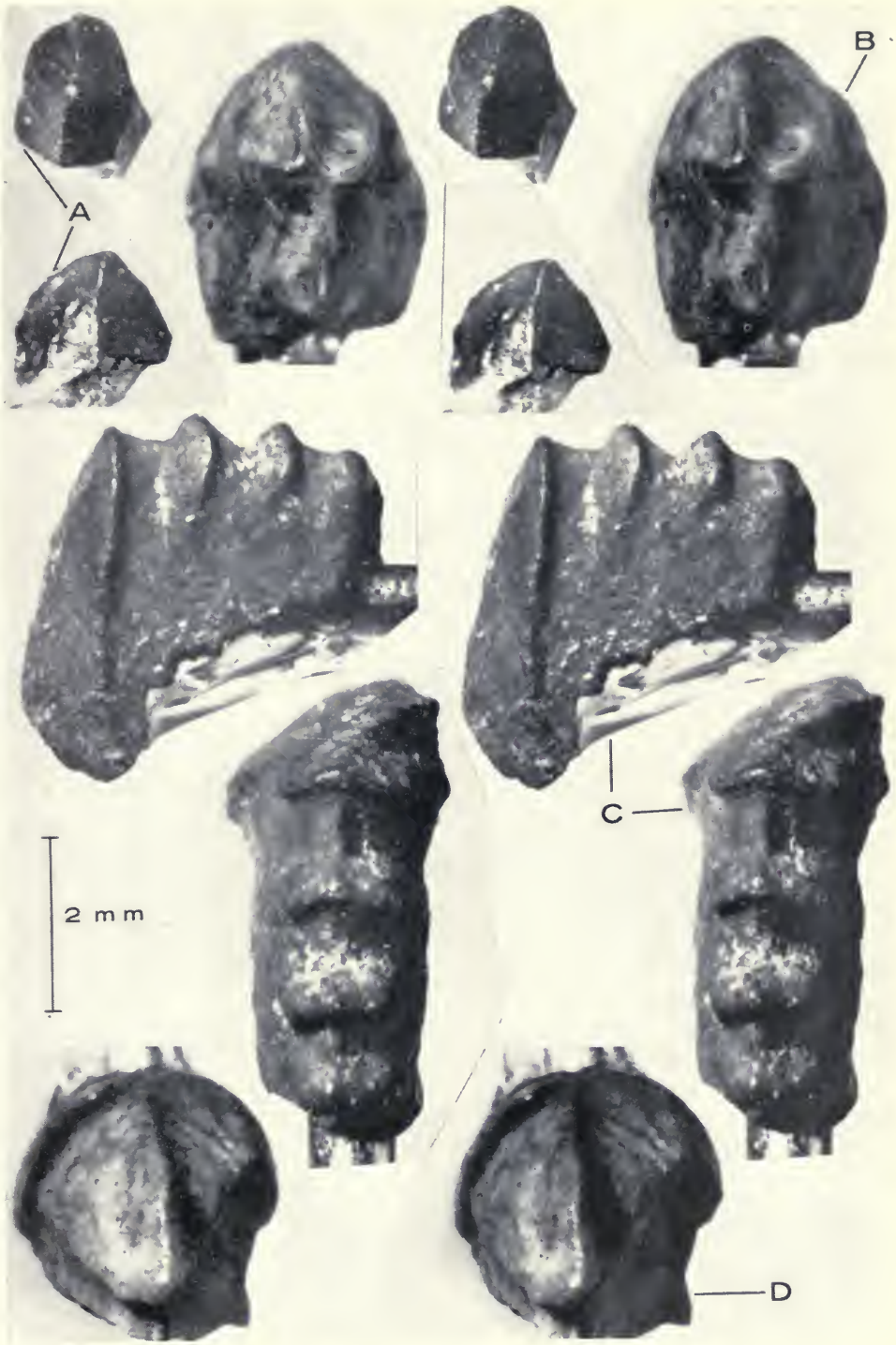
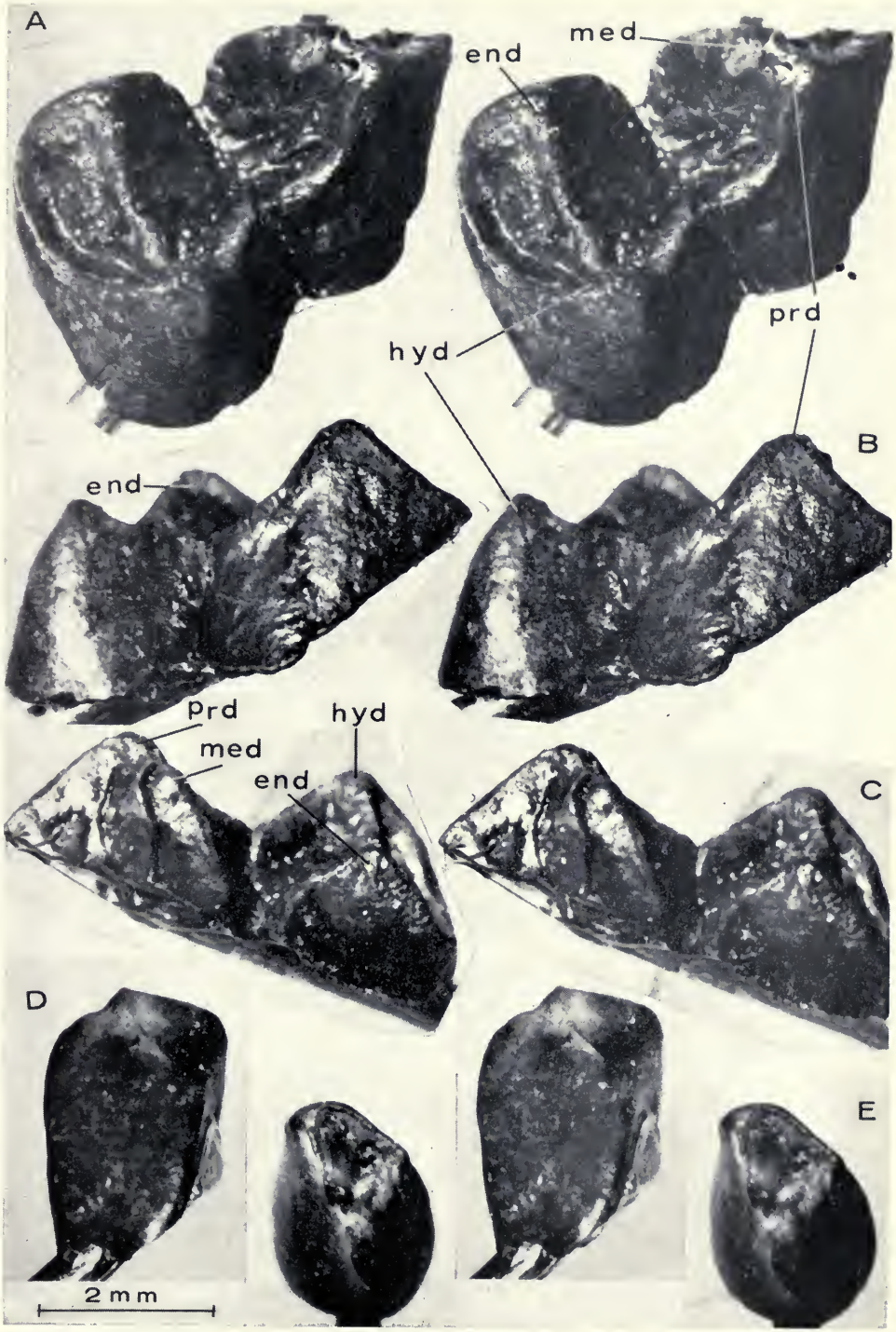

A
B
C
D
2 mm

PLATE III.—Teeth of two phalangerines. Scale approx. × 12½. Stereo relief slightly exaggerated. **A–C.** A tooth of uncertain generic affinities, ? *Phalanger*, or *Trichosurus*, or an unnamed related genus, PM 4555, a right M_T, crown, antero-lateral, and medial aspects. **D, E.** *Trichosurus* sp. indet., PM 4563, a left I^2, lateral and crown views.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end
med
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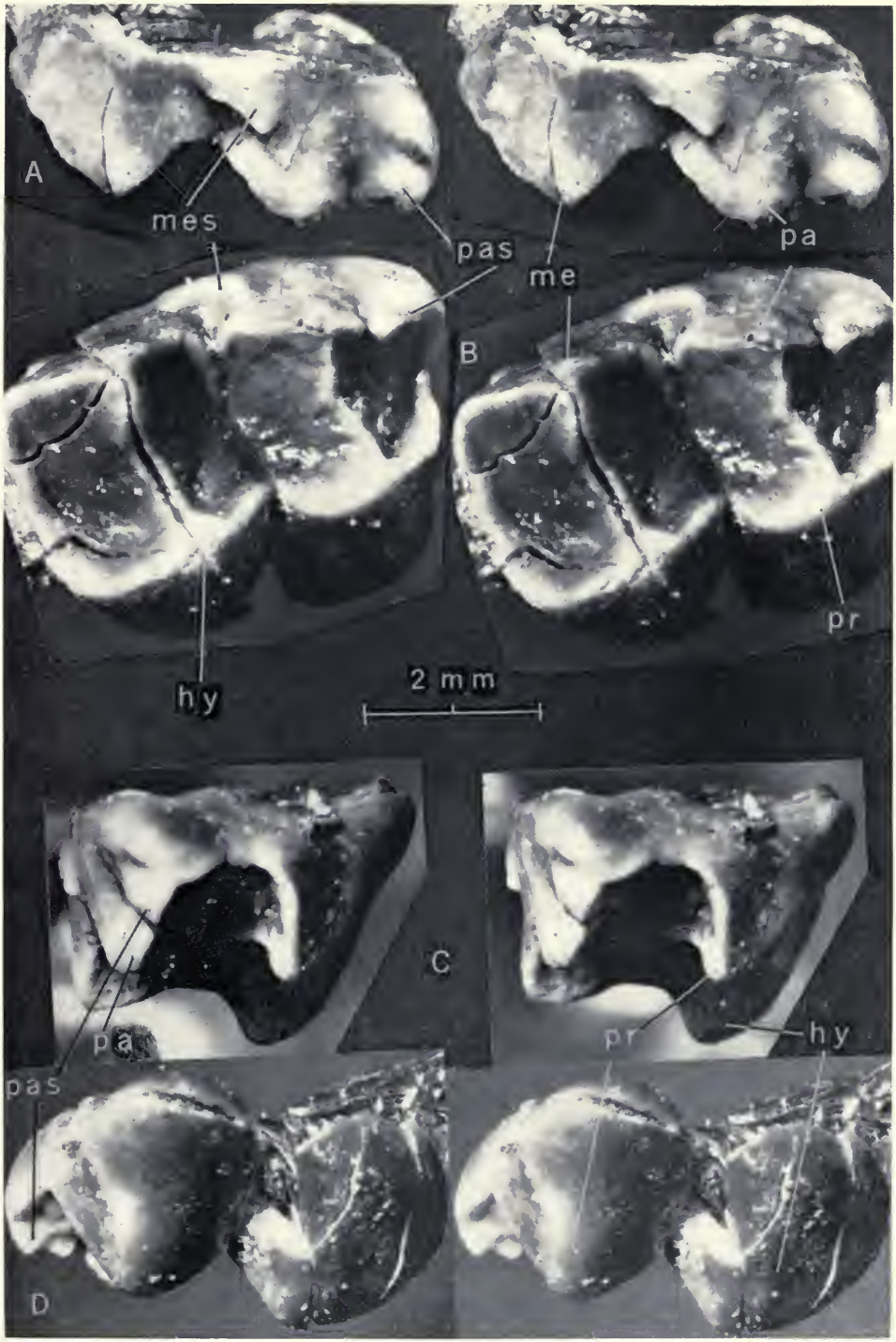
end
Prd
hyd
med
end
C
D
2 mm
E

PLATE IV.—Tooth of a phalangerine of uncertain generic affinities, ? *Phalanger*, or *Trichosurus*, or an unnamed related genus, PM 4571, a right M^1. Scale approx. × 13. **A, B.** Lateral and crown views. **C, D.** Anterior and medial views.


A
mes
pas
B
me
pa
pr
hy
2 mm
C
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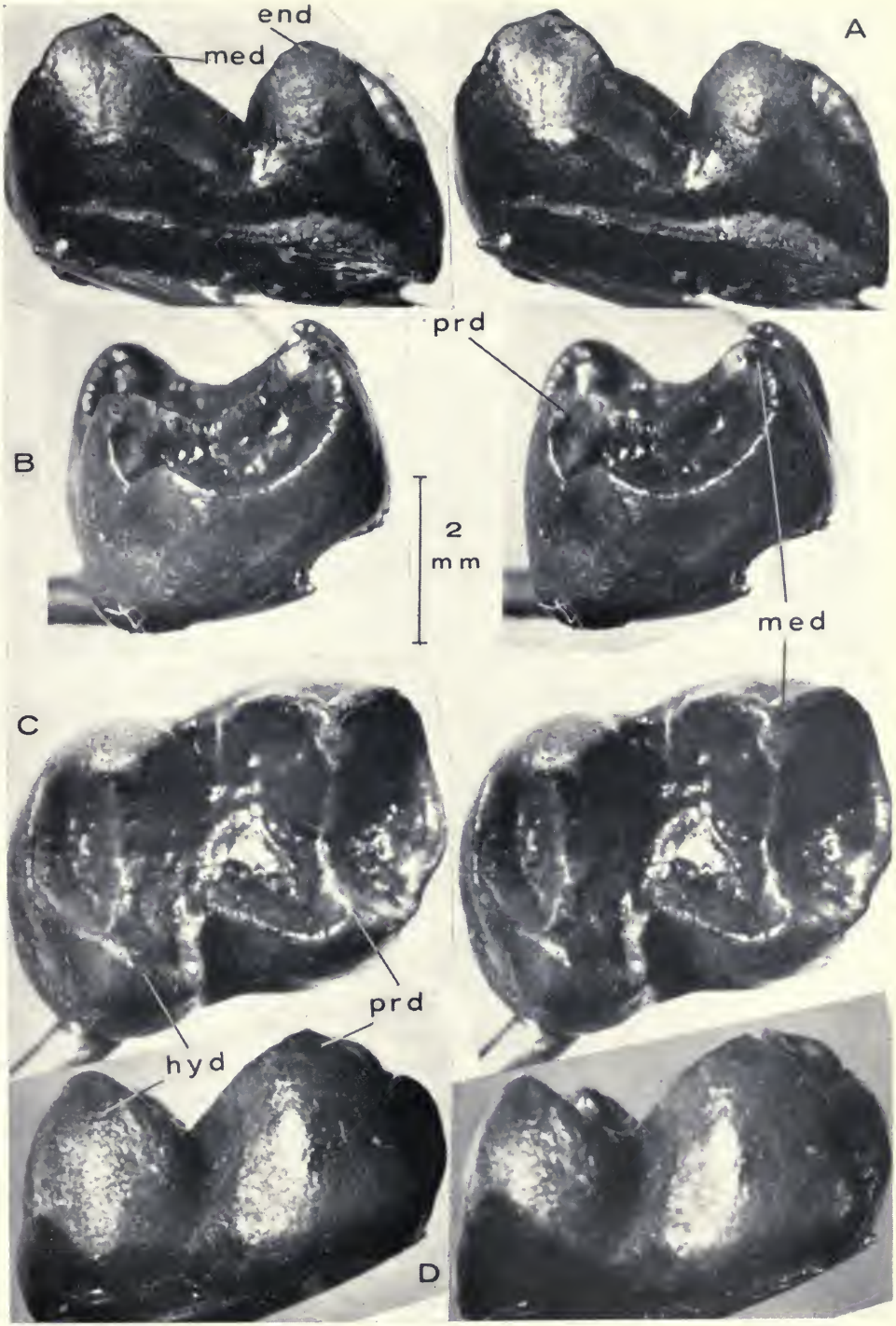
pas
D
pr
hy

PLATE V.—Right $M_{\overline{3}}$ of a phalangerine of uncertain generic affinities, ? *Phalanger*, or *Trichosurus*, or an unnamed related genus, NMV-P 26407. Scale approx. × 12. **A, B.** Medial and anterior views. **C, D.** Crown and lateral views.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C
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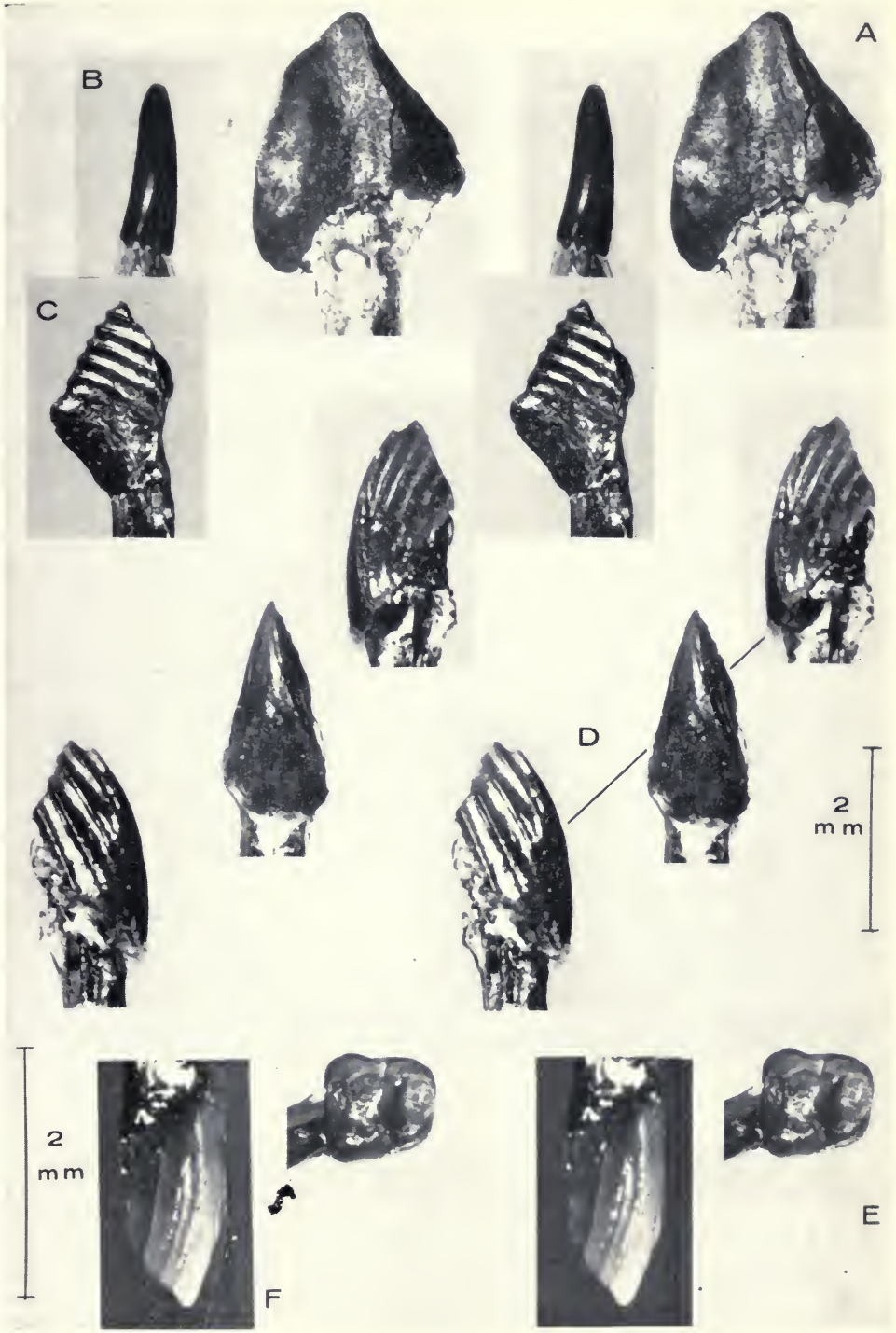
D

PLATE VI.—Teeth of several phalangerids and an indet. macropodine. **A.** Indet. macropodine, PM 4559, a partial left lower premolar, labial view. **B.** Indet. minute phalangerine, PM 4553, a left $I_{\bar{1}}$ in dorso-mesial (dorso-medial) view. **C.** *Burramys* sp., NMV-P26409, posterior three-fourths of a left $P_{\bar{4}}$, medial view. **D.** *Burramys* sp., PM 4439, anterior third to half of a right $P_{\bar{4}}$, lingual (top right), anterior (middle), and labial (bottom left) views. **E.** *Burramys* sp., PM 4470, a complete left M^2, crown view. Scale A–E approx. × 13. **F.** *Burramys* sp., PM 4459, fragment of a right P^4 preserving the antero-lingual corner of the tooth, lingual view. Scale F approx. × 18.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F

PLATE VII.—Teeth of *Pseudokoala erlita*, the large pseudocheirine from the Hamilton fauna. Scale approx. × 7½. **A, B.** NMV-P26399 (part of type). Left M^3, lateral (buccal) and crown views. **C.** NMV-P26399 (left), posterior view, and NMV-P26400 (also part of type), anterior view showing the matched interdental facets. **D, E.** Sketches of these facets as an aid to interpretation of the stereo photos shown in C. which proves the teeth to belong together.

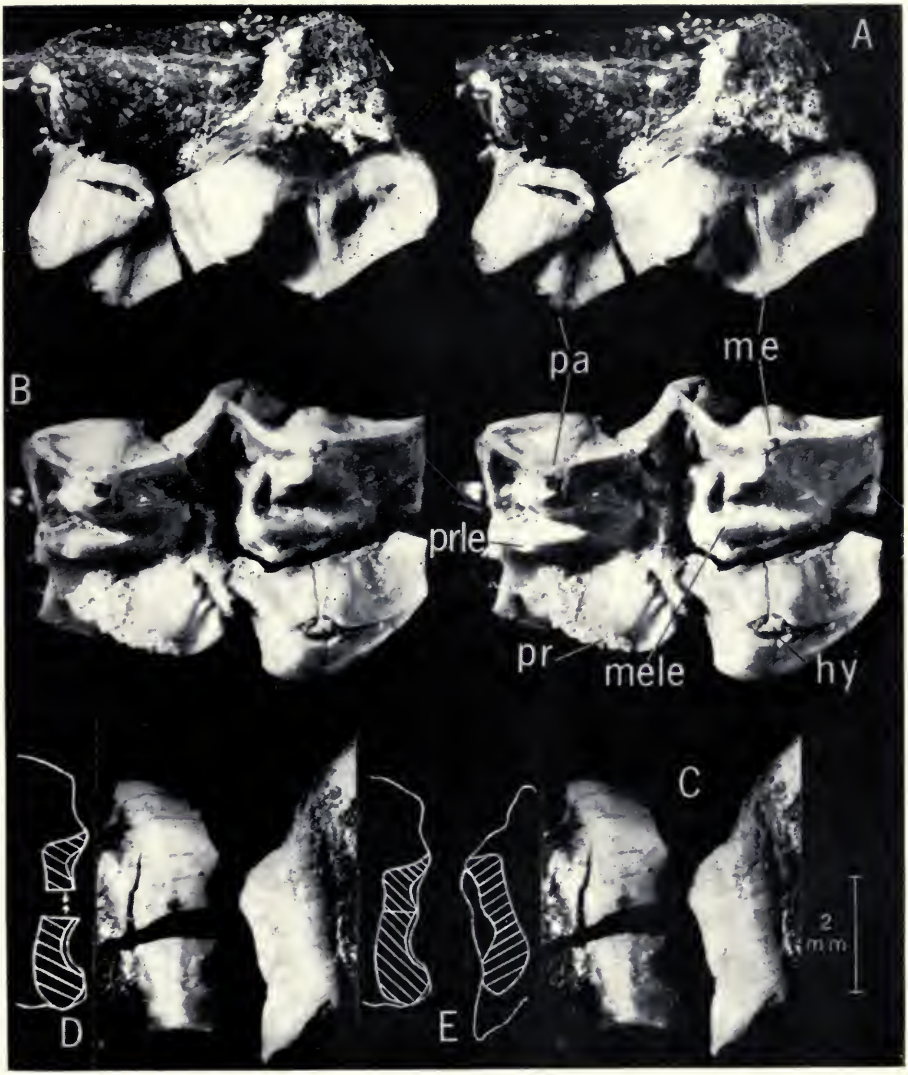
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PLATE VIII.—Teeth of pseudocheirines from the Hamilton fauna. Scale approx. × 11. A. and B. *Pseudokoala erlita*. **A.** NMV-P26400, the left M^4 (part of type) in occlusal view. **B.** PM 4588, anterior half of the left $M_{\overline{1}}$, dorsally oblique, antero-lateral view. C. & D. ? *P. erlita*. **C.** PM 4495, possibly the posterior half of a paracone, or metacone of an anterior molar, or more likely the back of a P^4. The view is a postero-medial oblique one for each of three alternative interpretations. **D.** PM 4496, the posterior half of a paracone seen in a comparable angle as in C.

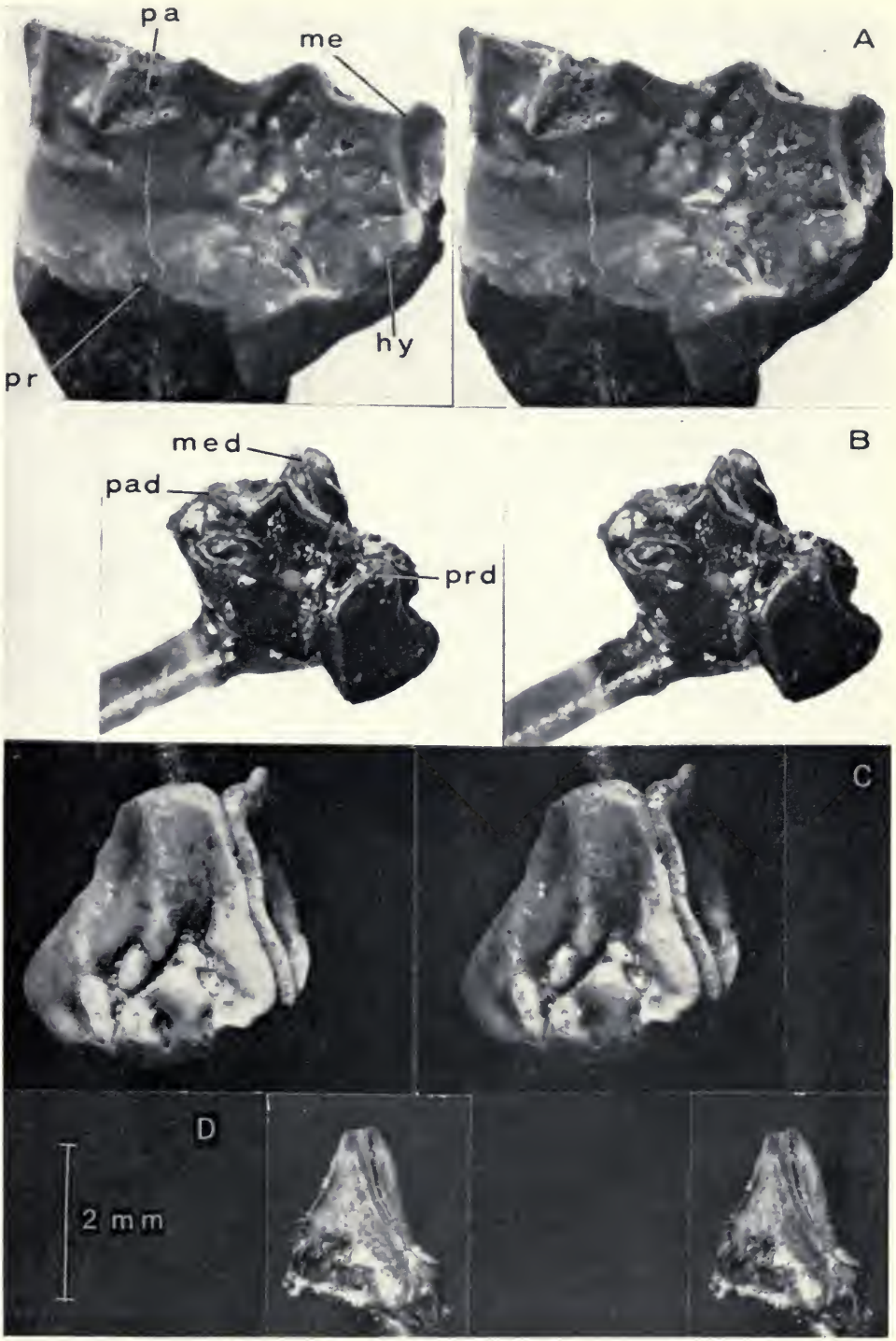
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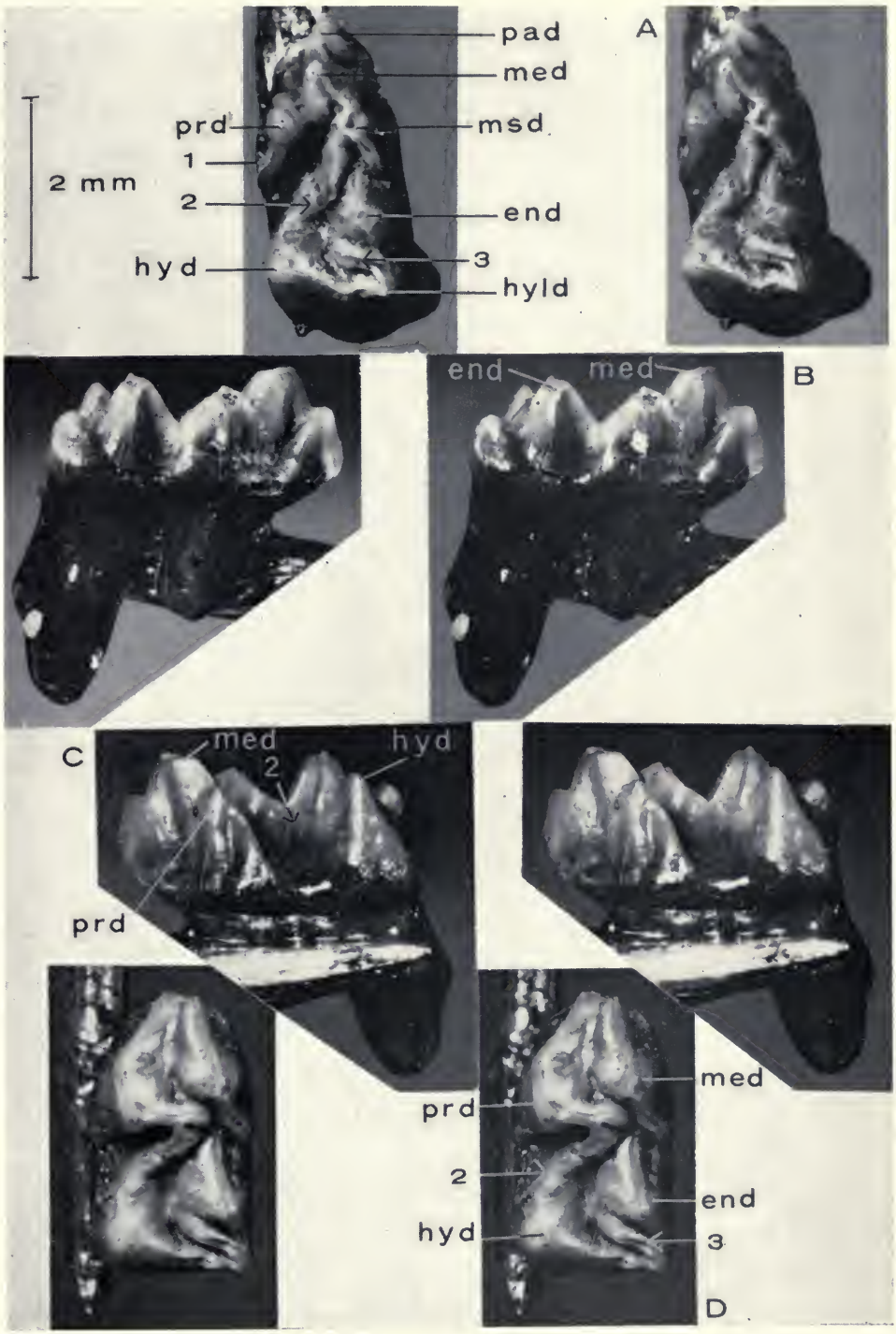
PLATE IX.—Teeth of *Pseudocheirus stirtoni*. Scale approx. × 13. **A–C.** Left $M_{\bar{1}}$, NMV-26401 (part of type), crown (A), medial (B), and lateral (C) views. **D.** Left M_2, NMV-P26402 (part of type), crown view. Numbered arrows correspond to the following scheme: (1) posterior crest of protoconid of $M_{\bar{1}}$; (2) hypolophid ridge; (3) entostylid ridge.


pad
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3
D

PLATE X.—Teeth of *Pseudocheirus stirtoni*. **A–C.** Left $M_{\bar{2}}$, NMV-P 26402 (part of type), medial (A), posterior (B), and lateral views. Scale approx. × 13. **D.** Left $M_{\bar{3}}$, NMV-P26403 (part of type), crown view. Arrow 4 indicates an interdental facet. Abbreviations 1, 2, 3 as in Plate IX. Scale approx. × 12.

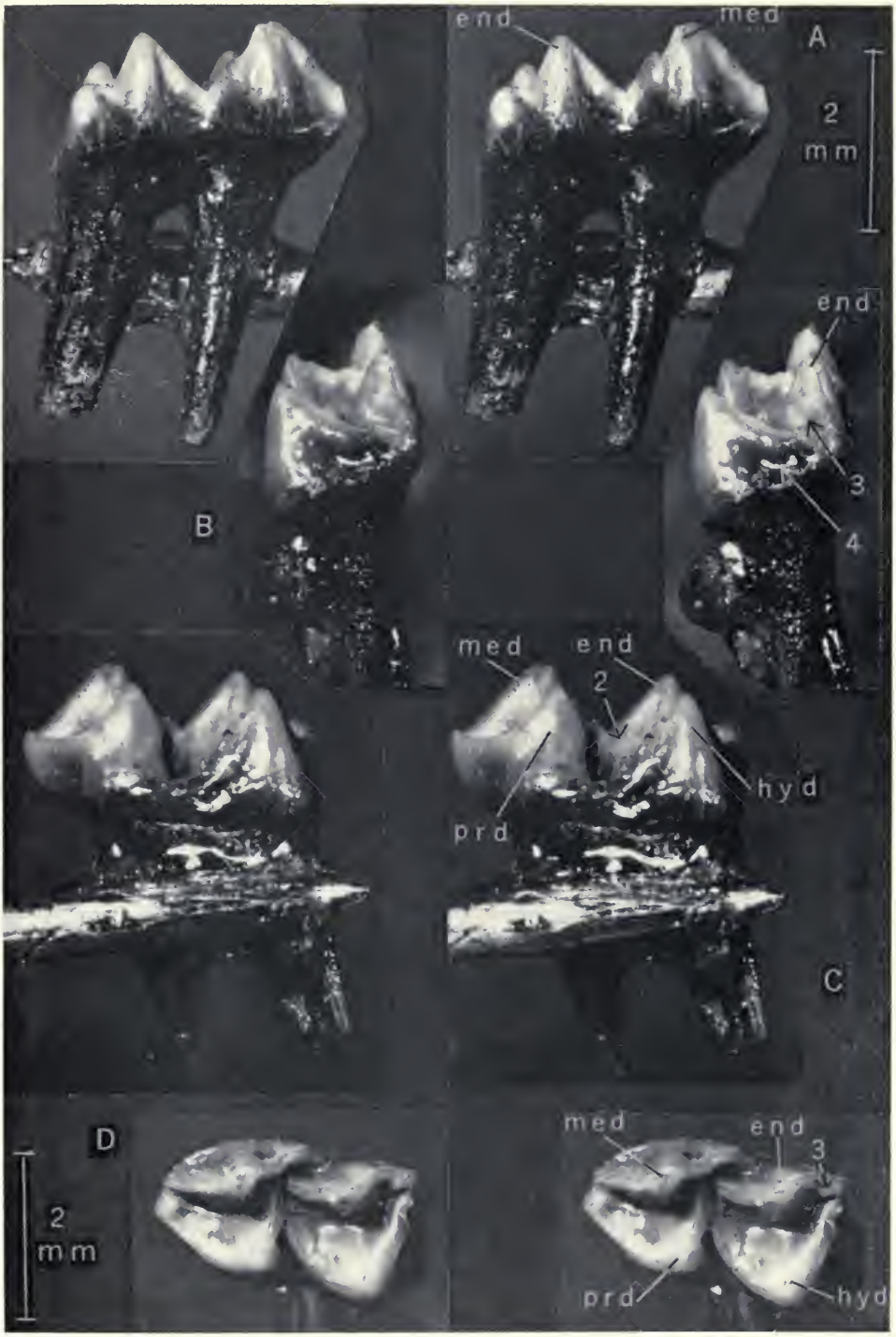

end
med
A
2
mm
end
3
4
B
med
end
2
hyd
prd
C
D
2
mm
med
end
3
prd
hyd

PLATE XI.—Teeth of *Pseudocheirus stirtoni*. **A–C.** Left $M_{\bar{3}}$, NMV-P26403 (part of type), lateral (A), anterior (B), and posterior (C) views. Scale approx. × 12. **D–E.** Left $M_{\bar{4}}$, NMV-P26404 (part of type), crown (D), and medial (E) views. Scale approx. × 13. Abbreviations 1, 2, 3 as in Plate IX.

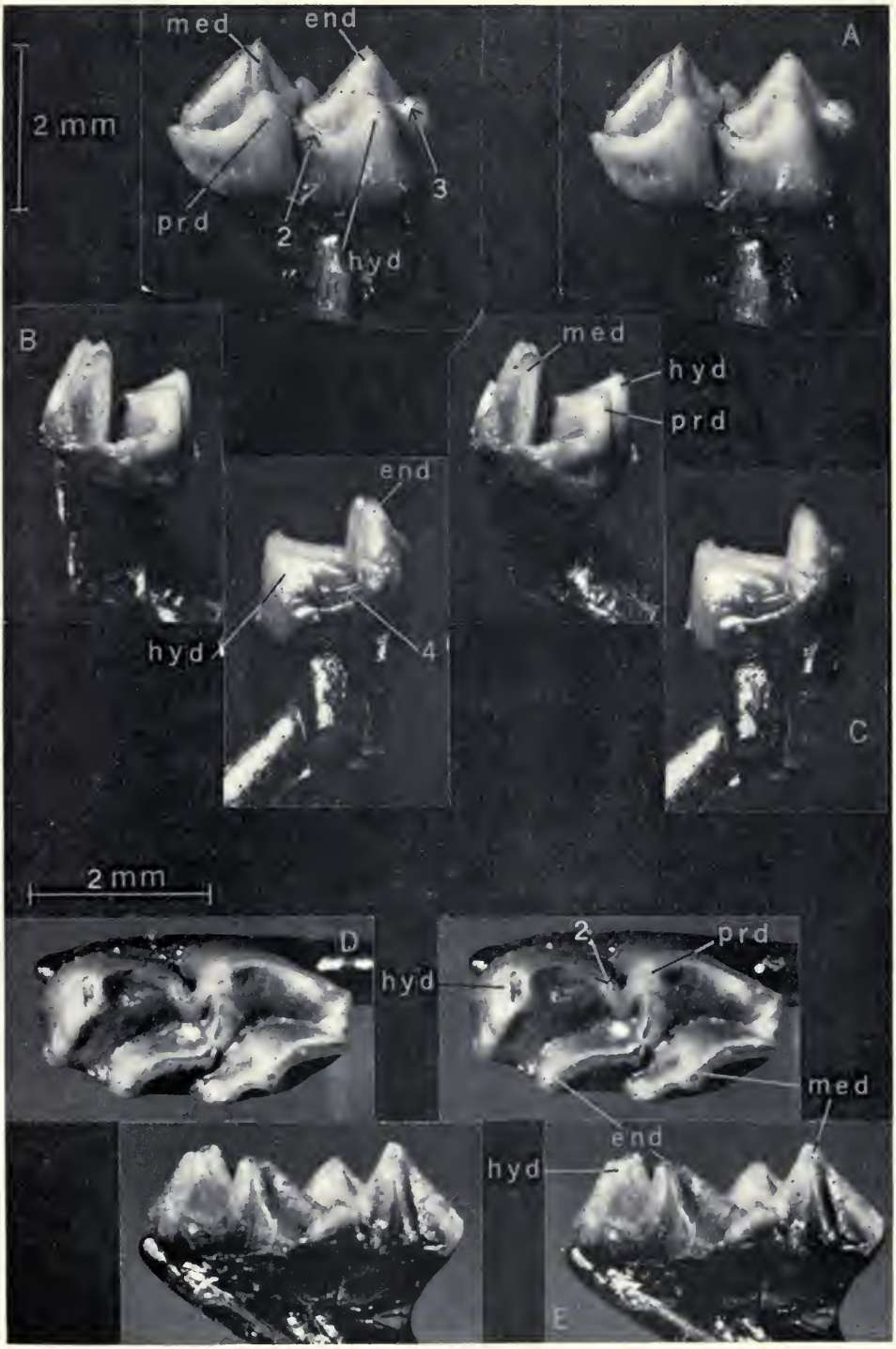

med
end
2 mm
prd
2
3
hyd
A
B
med
hyd
prd
end
hyd
4
C
2 mm
D
hyd
2
prd
med
end
hyd
E

PLATE XII.—Teeth of *Pseudocheirus stirtoni*. Scale approx. × 13. **A, B.** Left $M_{\bar{4}}$, NMV-P26404 (part of type), lateral (A) and posterior (B) views. **C–E.** Left $P_{\bar{4}}$, PM 4477, medial (C), lateral (D), and crown views. Arrows in C–E point to cleft between the major cusps discussed in text.

A
med
hyd
prd
med
end
hyd
B
C
D
E
2 mm

PLATE XIII.—Three upper cheek teeth of *Pseudocheirus stirtoni*. **A–C.** A left P^4 (PM 4549), lingual (A), crown (B), and labial (C) views. Scale approx. × 10. **D, E.** A left M^1 (or M^2) (PM 4542), labial (D) and crown views. Scale approx. × 13. **F.** A right M^1 (or M^2) (PM 4543), labial view. Scale approx. × 12½.

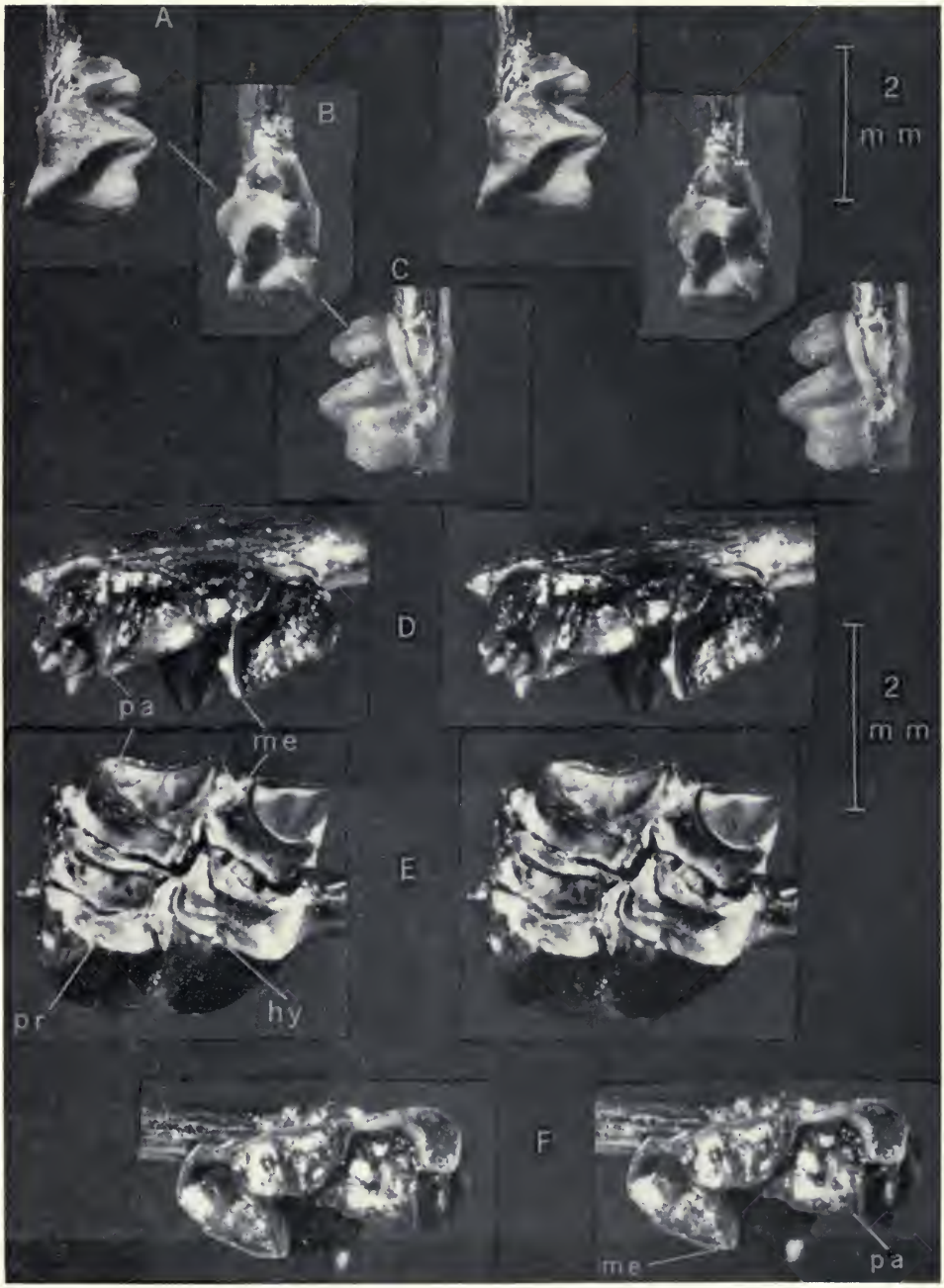

A
B
C
2
mm
D
pa
me
2
mm
E
pr
hy
F
me
pa

PLATE XIV.—Three upper molars of *Pseudocheirus stirtoni*. **A.** A right M^1 (or M^2) (PM 4543), crown view. Scale approx. × 13. **B–D.** A right M^2 (or M^3) (PM 4422), posterior (B), labial (C), and crown views. Scale approx. × 9. **E, F.** A right M^2 (or M^3) (NMV-P26410), labial (E), and crown views. Scale approx. × 13.

pa
A
2
mm
hy
pr
B
2 mm
C
pa
D
pr
E
2
mm
me
pa
hy
F

PLATE XV.—Three teeth of *Pseudocheirus marshalli*. Scale approx. × 13. **A.** PM 4591. A right $P_{\overline{4}}$, crown view. **B.** NMV-P26405, the type. A left $M^{\underline{1}}$ lacking the paracone, labial (above), and occlusal views. **C.** PM 4587. A left $M^{\underline{4}}$, labial (above) and occlusal views.

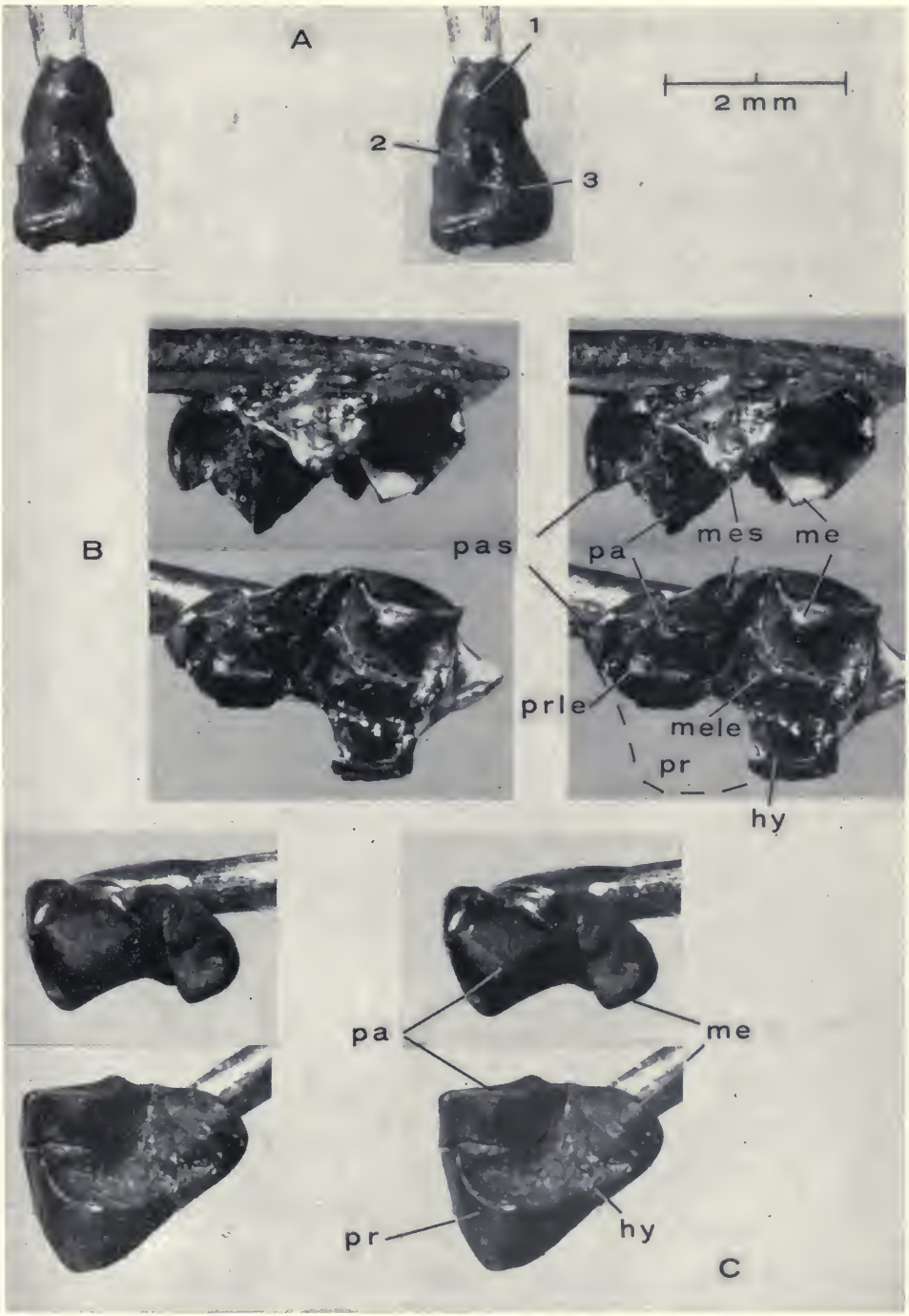

A
1
2
3
2 mm
B
pas
pa
mes
me
prle
mele
pr
hy
pa
me
pr
hy
C

PLATE XVI.—Three teeth of *Pseudocheirus marshalli*. **A.** PM 4423. A fragment of a left molar, probably M^1, crown view. Scale approx. × 9. **B.** PM 4455. Right $M_{\overline{1}}$, crown, lateral, and medial views. Arrow indicates separation of "entostylid ridge" from entostylid, one of the features that distinguishes *P. marshalli* from *P. stirtoni*. **C.** NMV-P26413. Right $M_{\overline{3}}$ (or $M_{\overline{2}}$), crown, lateral, and medial views. Scale of B and C approx. × 10.

pa
me
A
mele
2 mm
prd
hyd
med
pad
msd
end
esd
B
2 mm
med
prd
msd
C
hyd
end
hyd

PLATE XVII.—Teeth of *Pseudocheirus marshalli* and *Pseudocheirus* sp. indet. from the Hamilton fauna. **A.** PM 4453. Posterior two-thirds of a left lower molar (either $M_{\bar{2}}$ or $M_{\bar{3}}$) of *P. marshalli* preserving part of the trigonid and all of the talonid, occlusal (above, left), and posterior views. Arrow 1 points to the entostylid and arrow 2 to the minute hypoconulid. **B.** PM 4476. A right M_4 or *P. marshalli*, occlusal (above, left) and medial (-lingual) views. A and B shown at approx. × 12. **C.** PM 4472. A left $I_{\bar{1}}$ of *Pseudocheirus* sp. indet., dorsal and medial views. Scale approx. × 9.

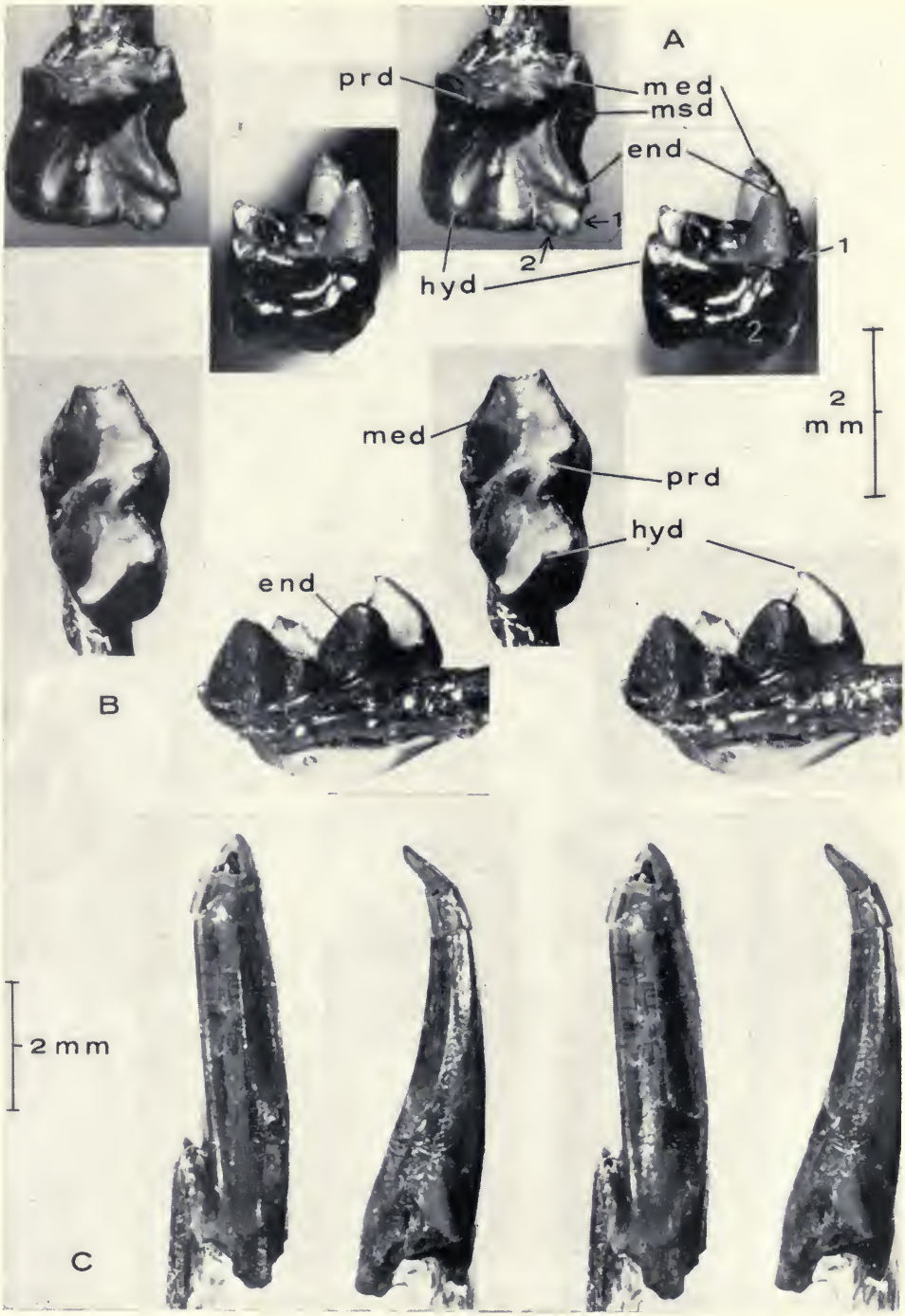

A
prd
med
msd
end
hyd
1
2
1
2
2 mm
med
prd
hyd
end
B
2 mm
C

PLATE XVIII.—Teeth of *Pseudocheirus* sp. indet., *Aepyrymnus* sp. indet., and *Hypsiprymnodon* sp. indet. **A.** NMV-P26415. A left I_1 of *Pseudocheirus* sp., dorsal (left) and near-medial views. **B.** PM 4492. Fragment of left upper molar referred to *Aepyprymnus* sp. preserving the metacone and part of the hypocone. The fragment is shown in its posterior (top, right) and occlusal aspects. Arrows point to the posterior "cingulum." Scale of A and B approx. × 10. **C.** PM 4575. Anterior half of a right M^1 referred to *Hypsiprymnodon* sp., labial (top) and occlusal views. Arrows indicate anterior cingulum. Scale approx. × 12½.

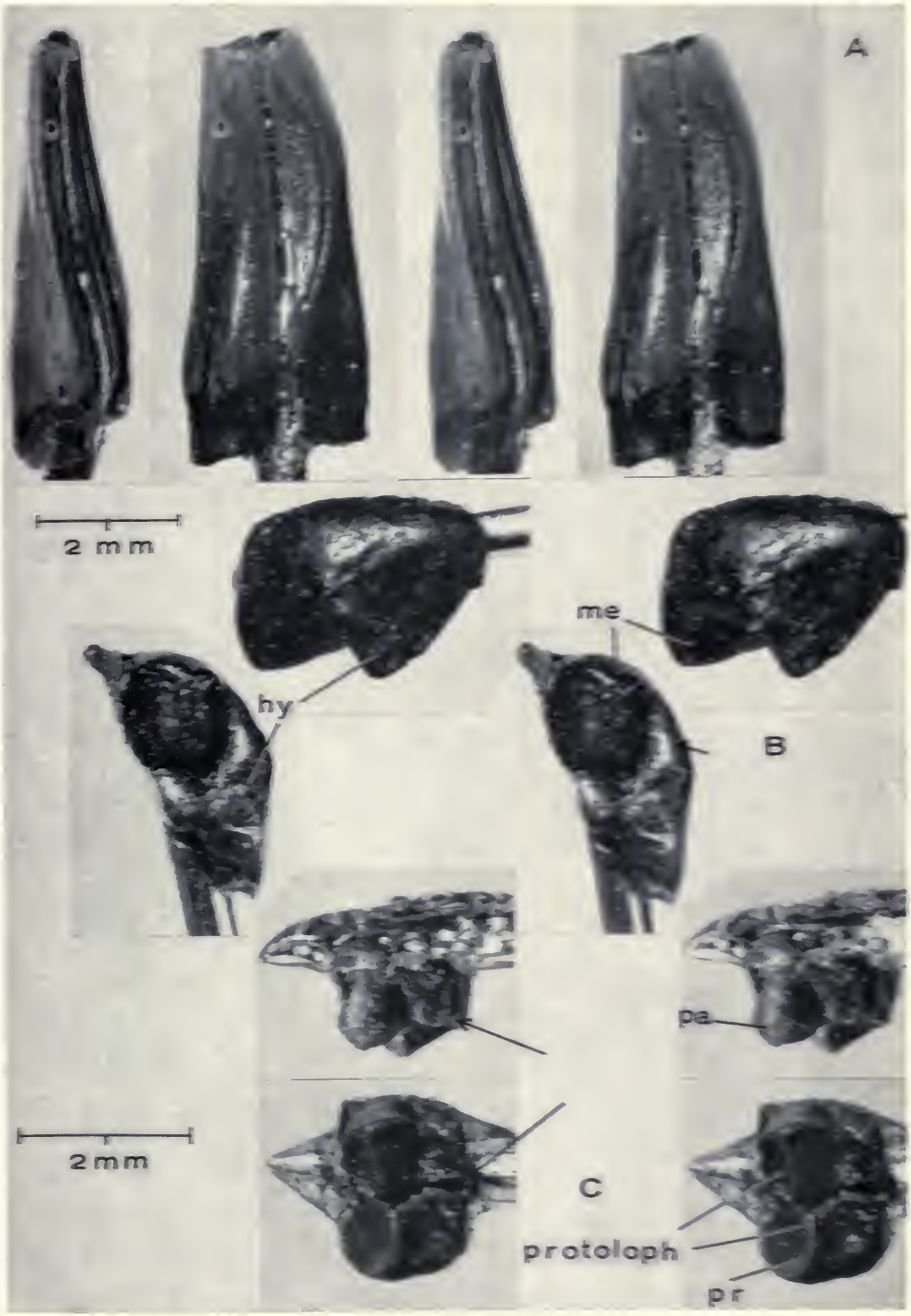

A
2 mm
hy
me
B
pa
2mm
C
protoloph
pr

PLATE XIX.—Partial premolar of a macropod, *Dorcopsis* sp. indet., from the Pliocene, Hamilton fauna, PM 4436. Posterior third of a right P^4. Scale approx. × 12. **A.** Occlusal view. **B.** Lingual view. **C.** Posterior view. **D.** Labial view.

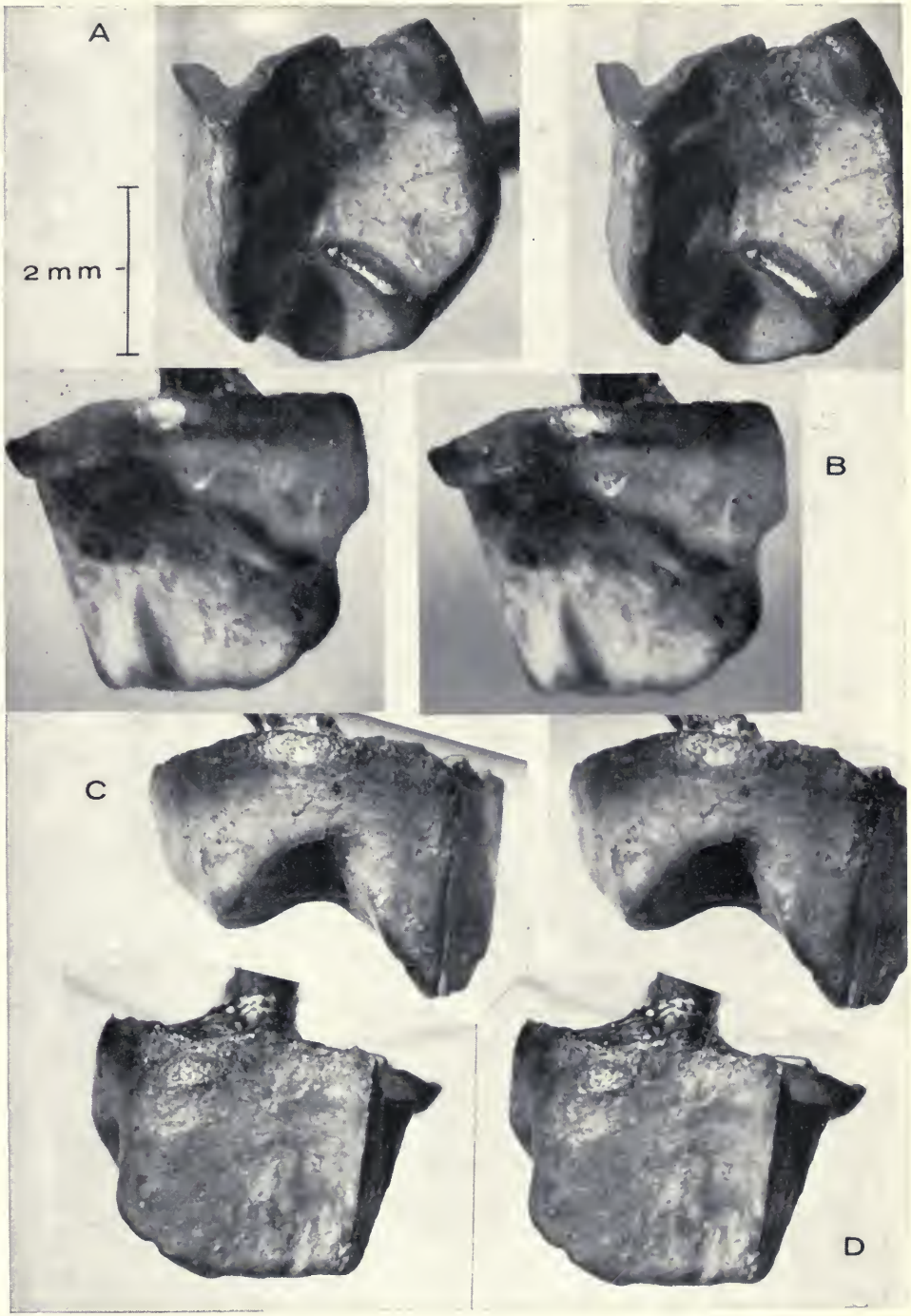

A
2 mm
B
C
D

PLATE XX.—An upper molar of the macropod, *Dorcopsis* sp. indet., PM 4433. Scale approx. × 8. **A.** Anterior view. **B.** Labial view. **C.** Occlusal view. **D.** Lingual view. **E.** Posterior view. Numbers 1 and 2 indicate the protoloph and metaloph.

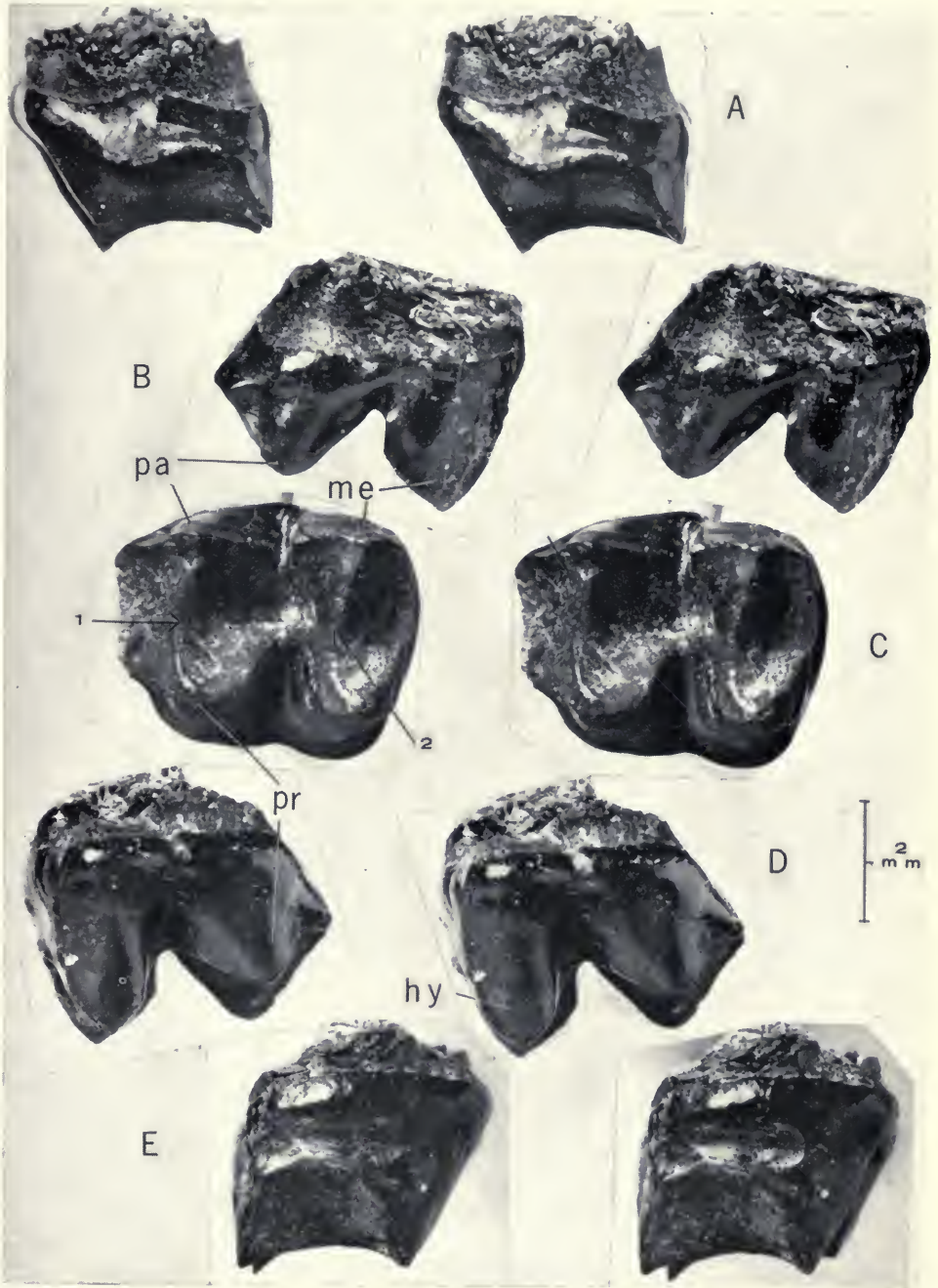

A
B
pa
me
1
2
C
pr
D
2
mm
hy
E

PLATE XXI.—NMV-P26417, a right upper molar of the macropod, *Dorcopsis* sp. indet. Scale approx. × 9. **A.** Anterior view. **B.** Labial view. **C.** Crown view. **D.** Posterior view. The arrow indicates the procingulum.

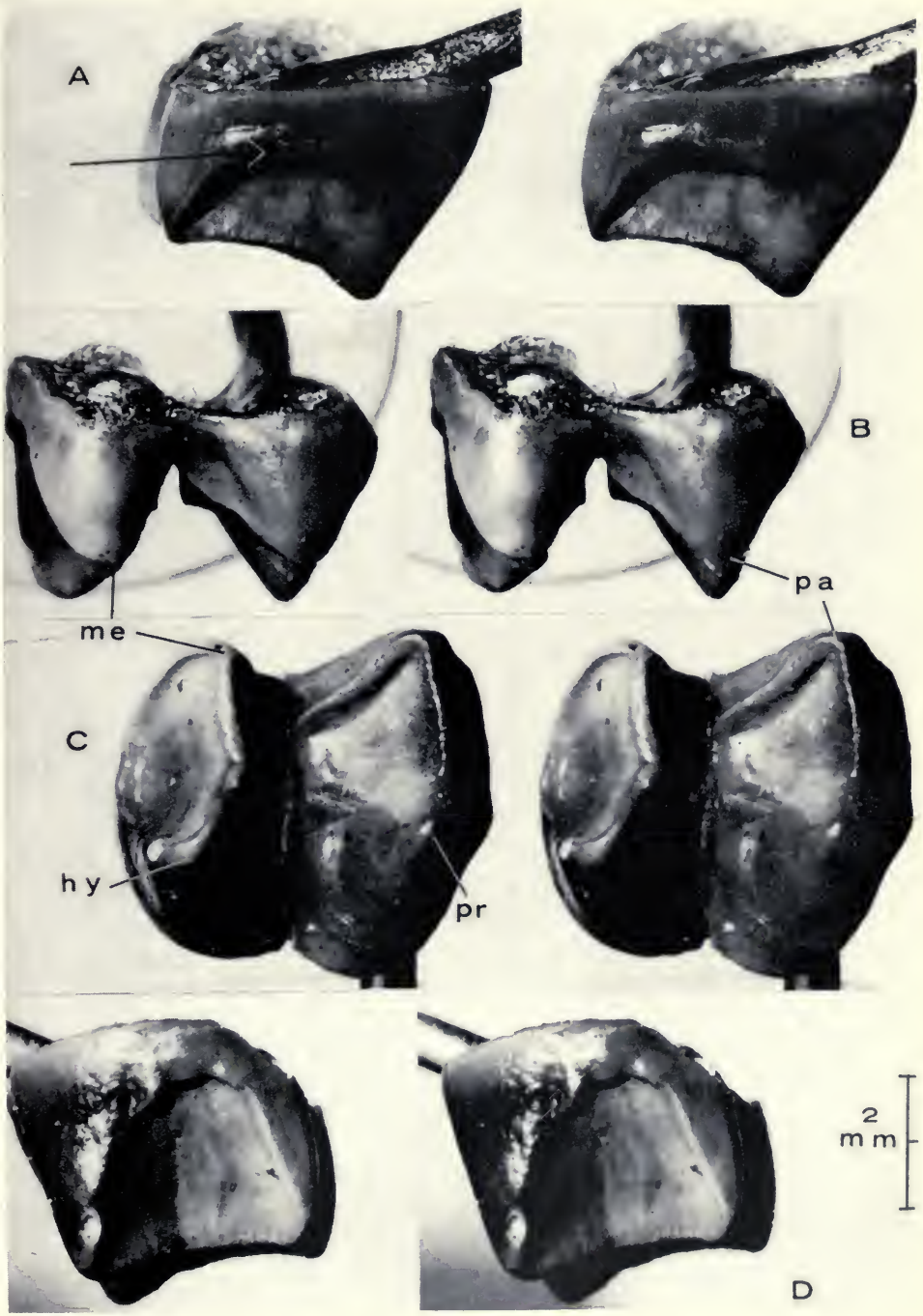

A
B
me
pa
C
hy
pr
2
mm
D

PLATE XXII.—Right upper molar of *Dorcopsis* sp. indet., PM 4434. Scale approx. × 10. **A.** Anterior view. **B.** Labial view. **C.** Crown view. **D.** Posterior view. The arrow indicates the procingulum.

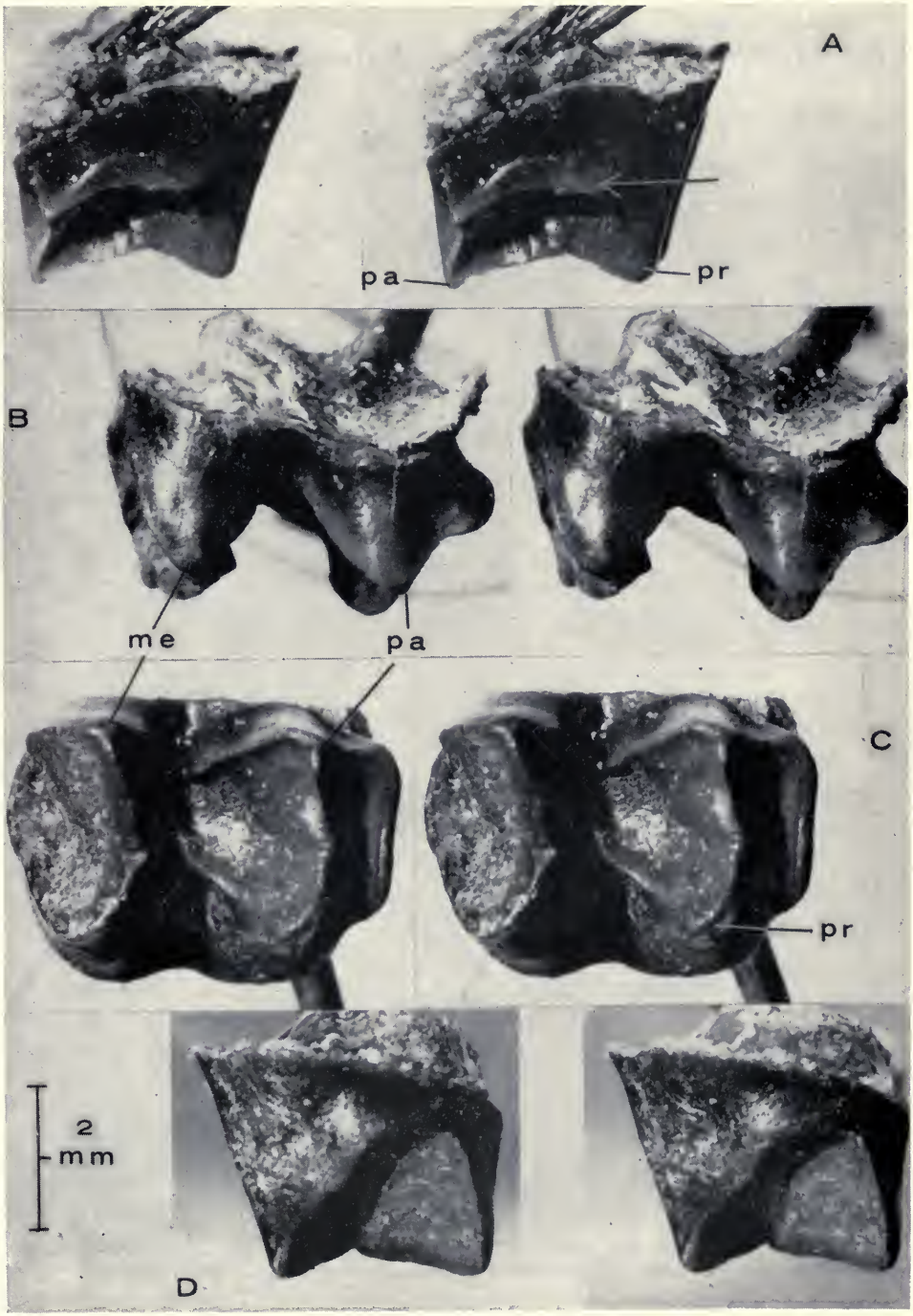

A
pa
pr
B
me
pa
C
pr
2
mm
D

PLATE XXIII.—Two lower molars referred to two genera of macropods in the Hamilton fauna. **A.** *Dorcopsis* sp., PM 4565, a nearly complete right molar lacking the tip of the protoconid and most of the hypoconid, crown view. Scale approx. × 9. **B–E.** *Thylogale* sp., PM 4564, a right molar, anterior (B), crown (C), lingual (D), and labial (E) views. ant cing=anterior cingulum. Scale approx. × 7½.

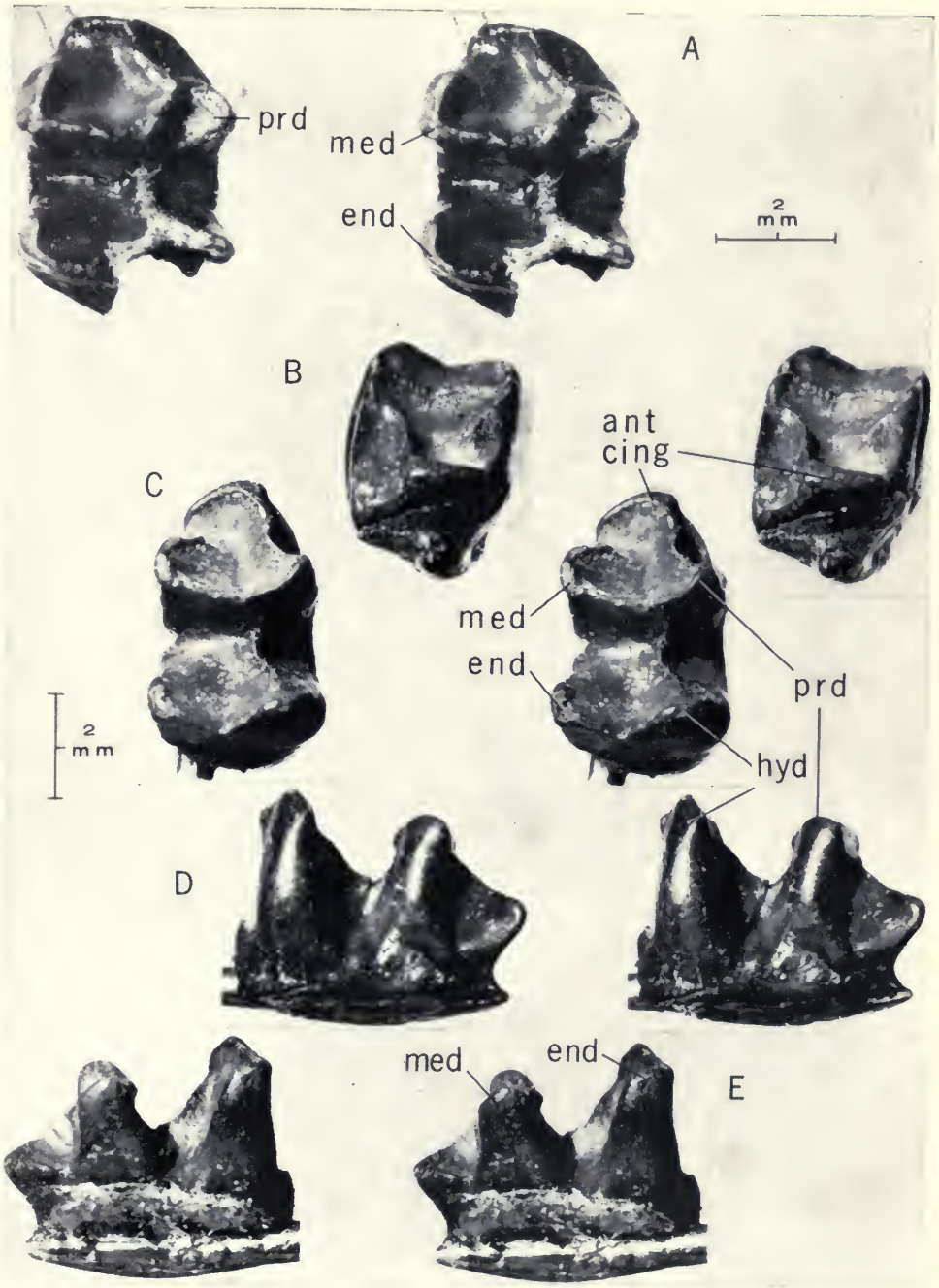

A
prd
med
end
2
mm
B
ant
cing
C
med
end
prd
hyd
2
mm
D
med
end
E

PLATE XXIV.—Two macropod teeth referred to *Thylogale* sp. indet. of the Hamilton fauna. Scale approx. × 7. **A–D.** PM 4576, a right lower molar, anterior (A), crown (B), lingual (C), and labial (D) views. **E, F.** PM 4432, the anterior half of a right lower molar, anterior (E) and crown (F) views.

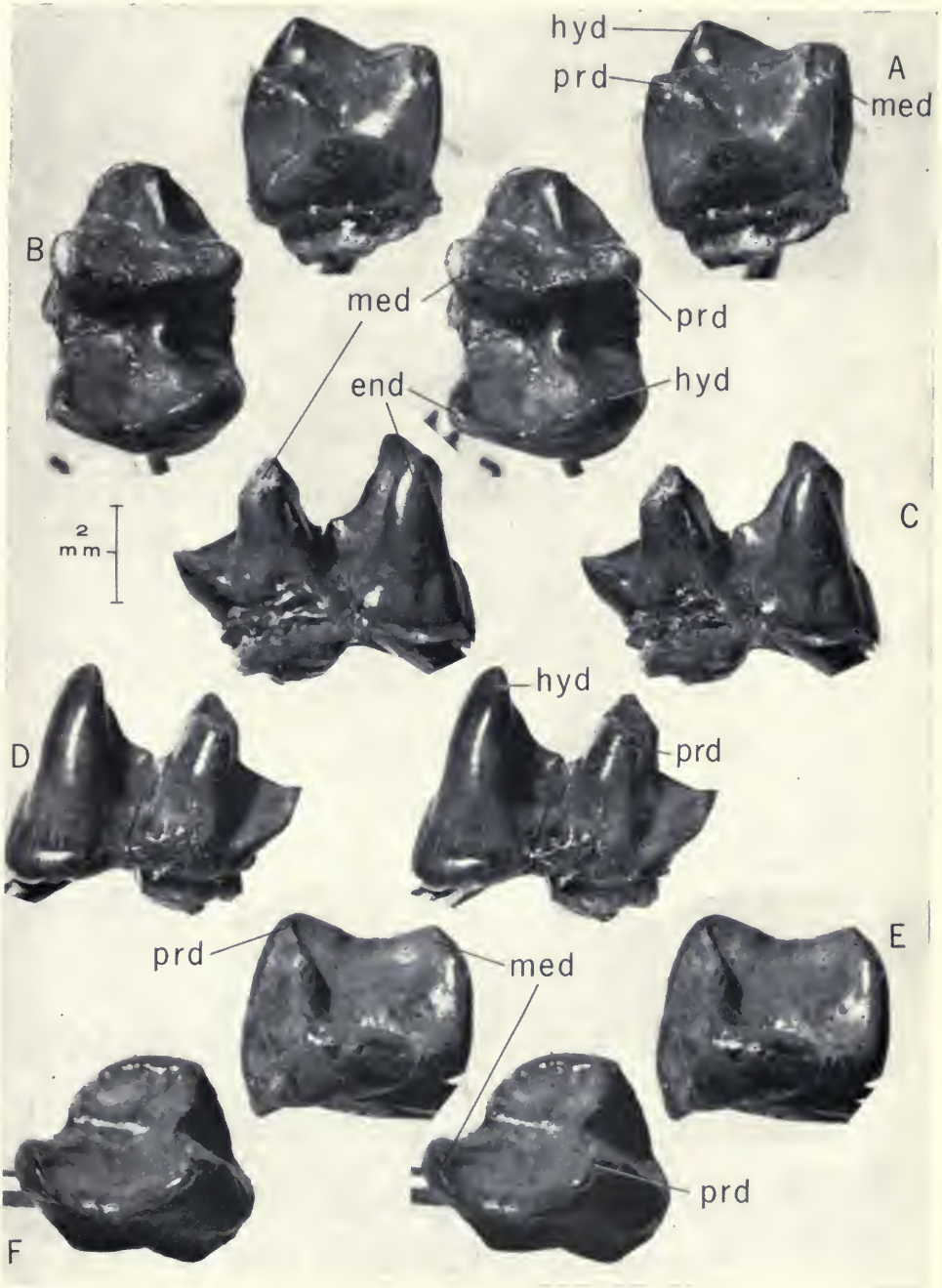

hyd
prd
A
med
B
med
prd
end
hyd
2
mm
C
hyd
D
prd
prd
med
E
prd
F

PLATE XXV.—Three macropod incisor teeth referred to *Thylogale* sp. indet. from the Hamilton fauna. Two are shown compared directly with corresponding teeth of the Recent *T. billiardieri*. **A.** Comparison of right I^3's of the Recent *T. billiardieri*, FM 81526 (left), and PM 4731 (right), ventro-lateral oblique views. **B.** Comparison of left I^3 of *T. billiardieri* (left) with a partial right I^3, PM 4731 (right), oblique view of occlusal surfaces. **C.** PM 4733, a left I^2, antero-lateral, oblique view. Scale of A–C approx. × 7. **D.** (Right) PM 4444, a left $I_{\bar{1}}$, ventro-lateral view, compared with the left $I_{\bar{1}}$ of *T. billiardieri* (left), FM 81526. Scale approx. × 2½.

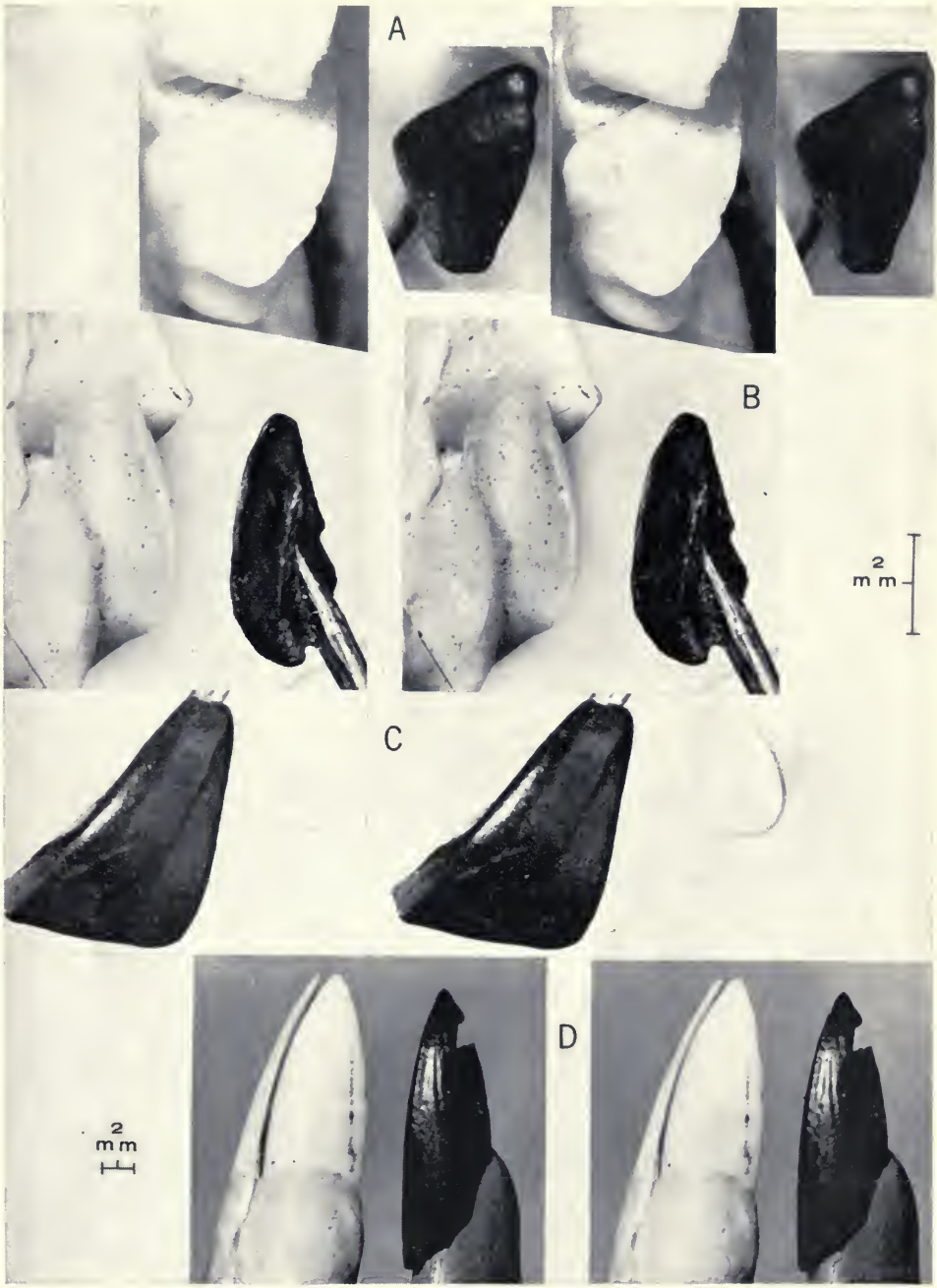

A
B
C
D
2 mm
2 mm

PLATE XXVI.—A deciduous lower molar tooth, PM 4438, referred to *Thylogale* sp. indet.: crown (A), posterior (B), lingual (C), and labial (D) views. Scale approx. × 11.

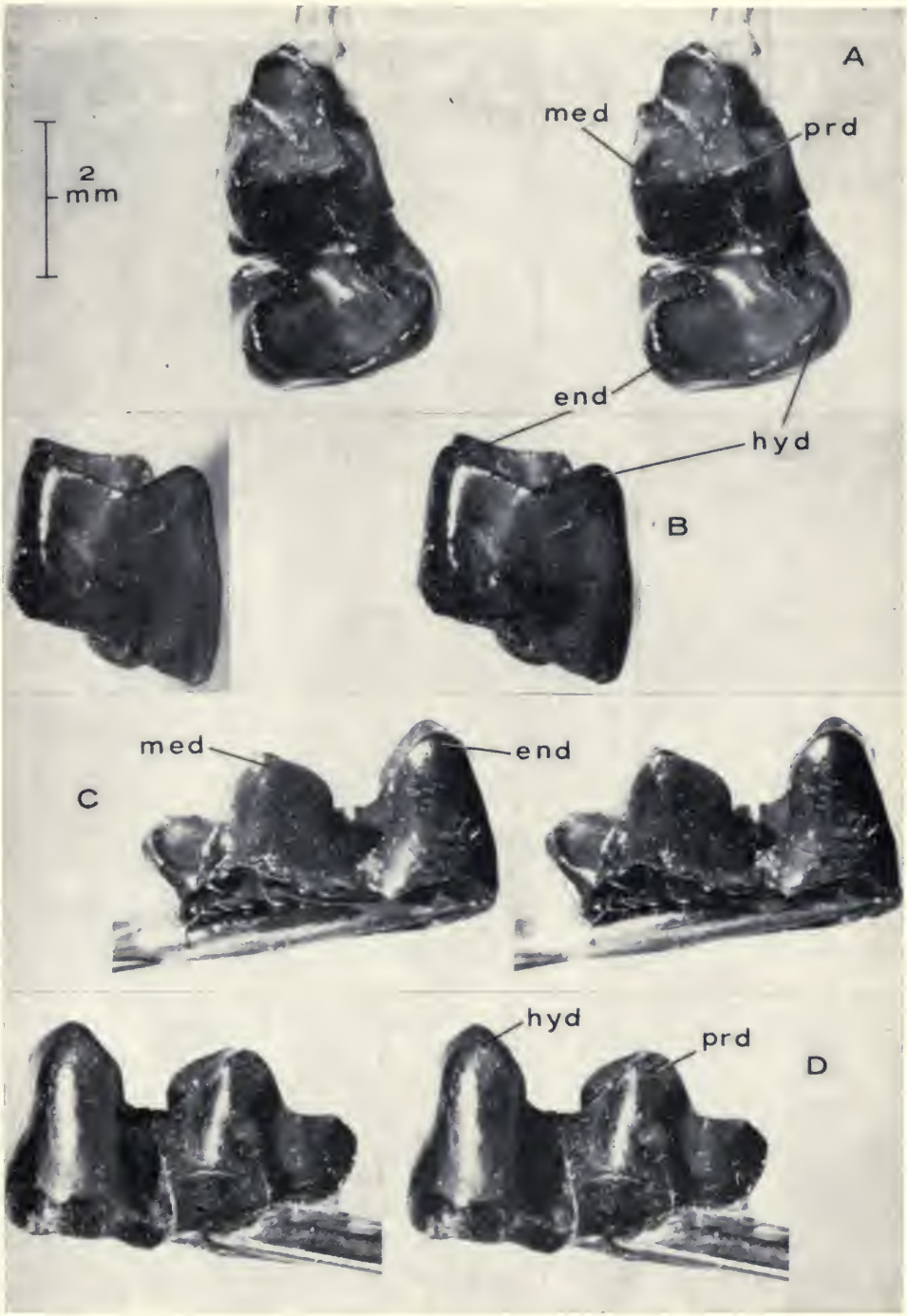

2
mm
A
med
prd
end
hyd
B
C
med
end
hyd
prd
D

PLATE XXVII.—Two macropod teeth and one tooth of an undetermined marsupial (C) from the Hamilton fauna. Scale approx. × 11. **A.** PM 4562. The posterior half of a premolar blade of *Thylogale* sp. indet., labial, lingual, and crown view. Identification is uncertain, specimen thought to be a $P_{\overline{3}}$ or $P_{\overline{4}}$. **B.** PM 4558. Posterior half of a premolar blade of an indet. macropodine, crown and side views. **C.** PM 4580. Fragment of a tooth as yet undetermined.

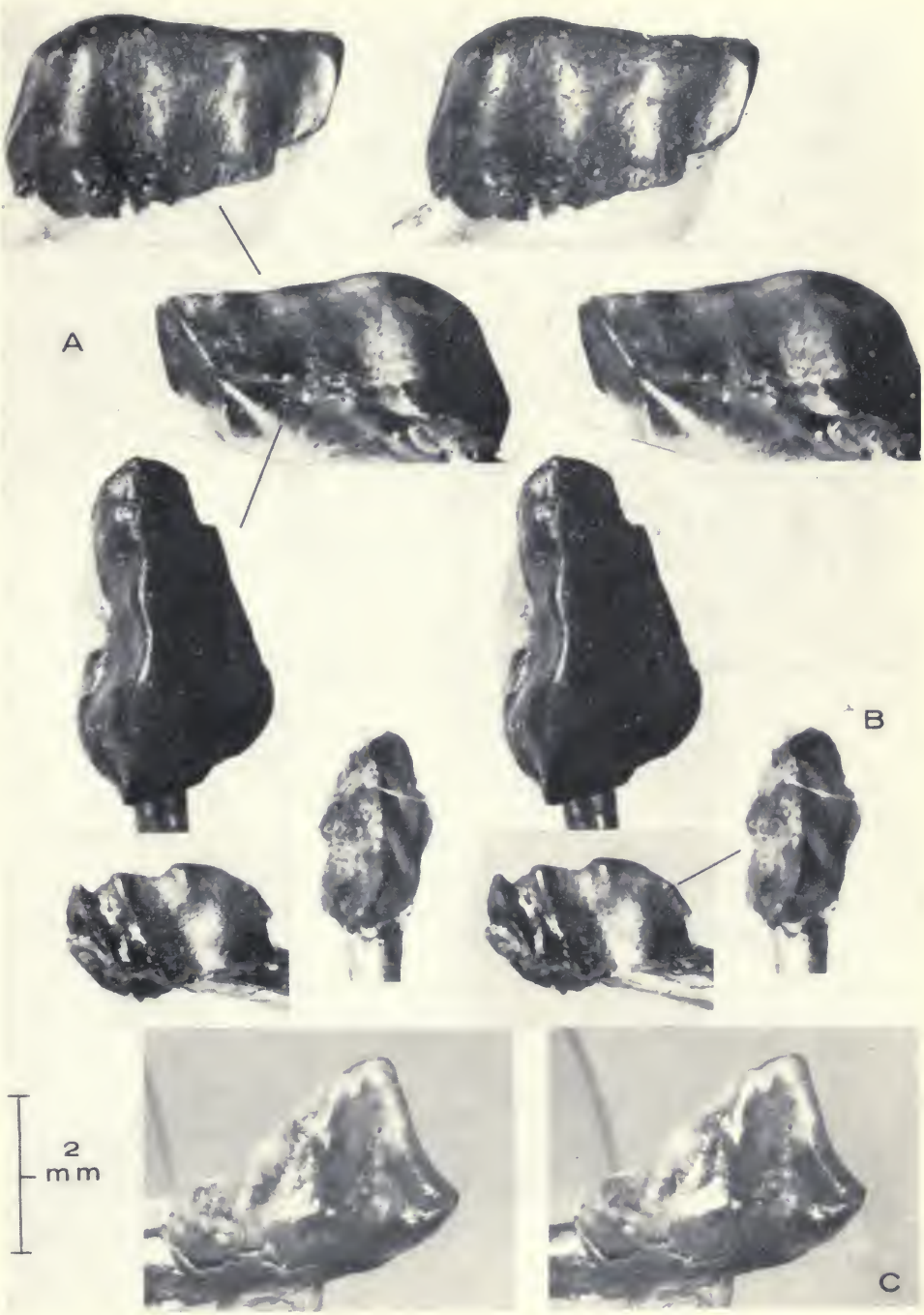

A
B
2
mm
C

PLATE XXVIII.—Two teeth referred to Macropodinae, *Incertae sedis* (large-sized form, probably a *Protemnodon*) from the Hamilton fauna. **A–E.** PM 4429, a left upper molar or a dP^4 in anterior (A), crown (B), labial (C), lingual (D), and posterior (E) views. **F.** PM 4498, a fragment of a worn right upper molar, anterior view. Scale approx. × 4½.

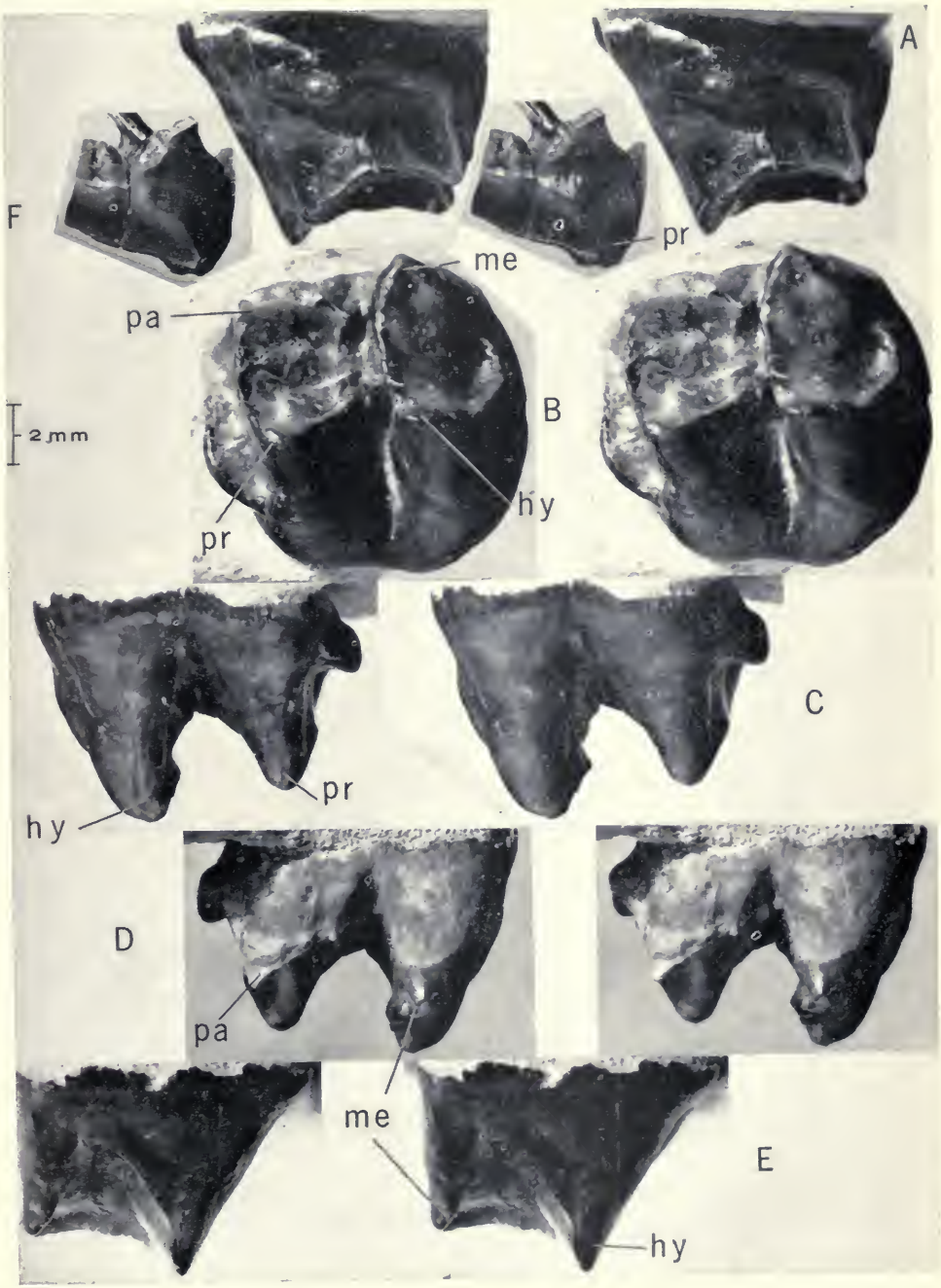

A
F
pr
me
pa
B
2 mm
hy
pr
C
pr
hy
D
pa
me
E
hy

PLATE XXIX.—Various tooth fragments referred to the Marsupialia are shown in Figures A–G, and the one placental speciman in the fauna, a bat, is shown in Figure H. Specimens in A–G all appear to be referrable to either Macropodinae, Potoroinae, or Phalangeridae. They have sufficient morphology that eventually more positive identification may be possible. Scale approx. × 11. **A.** PM 4593 **B.** PM 4582. **C.** PM 4730. **D.** PM 4595. **E.** PM 4560. **F.** PM 4594. **G.** NMV-P26424.

The bat (PM 4458), a microchiropteran, consists of a left ramus fragment with one molar tooth in place. Scale approx. × 12.

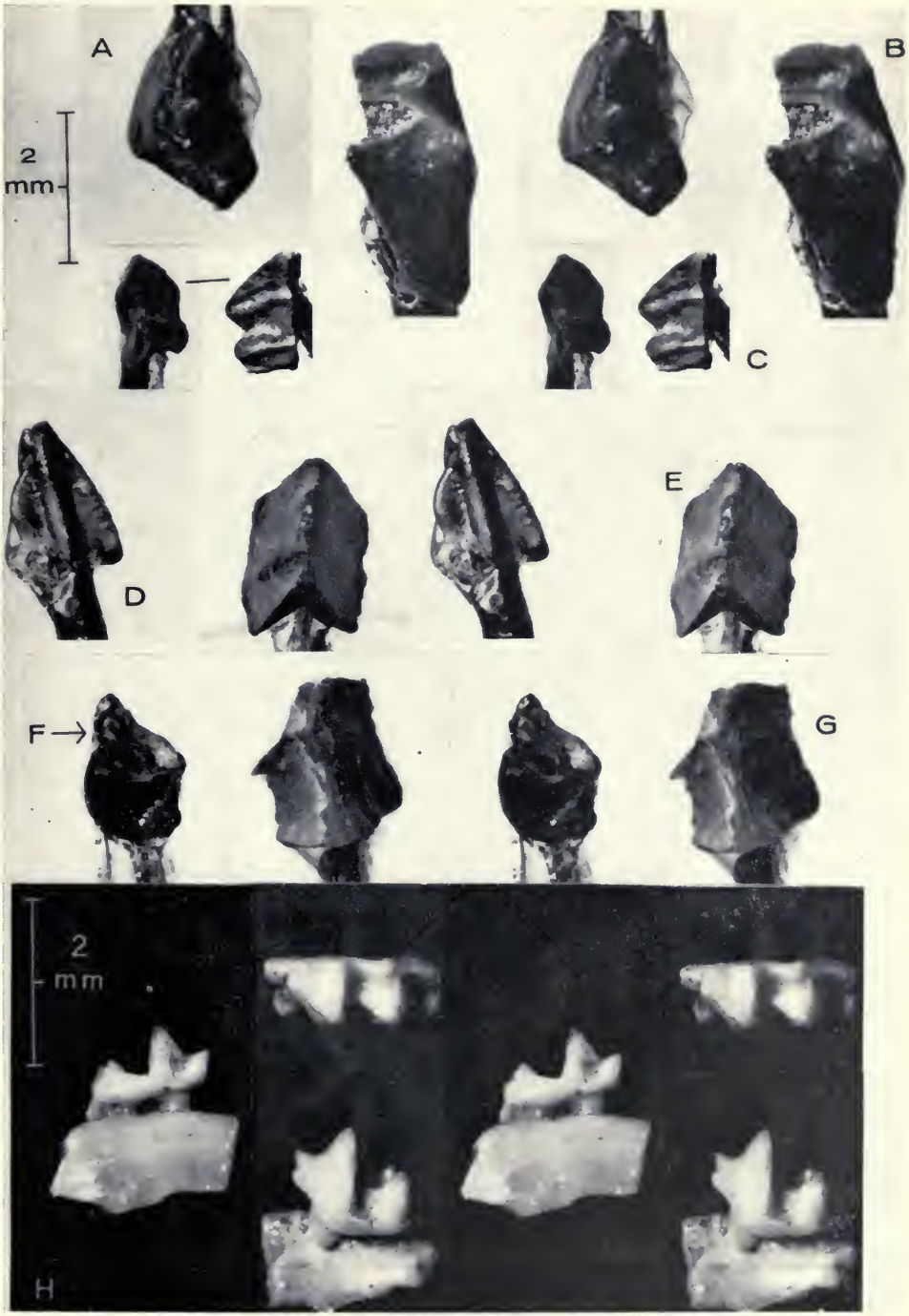

A
B
2
mm
C
D
E
F
G
2
mm
H

PLATE XXX.—A left lower molar, probably M_1 (or M_2) of a *Palorchestes* c. f. *painei* (PM 16801), the only diprotodont recovered from the Pliocene, Hamilton fauna; anterior (A), crown (B), posterior (C), lingual (D), and labial (E) views. Scale approx. × 2½.

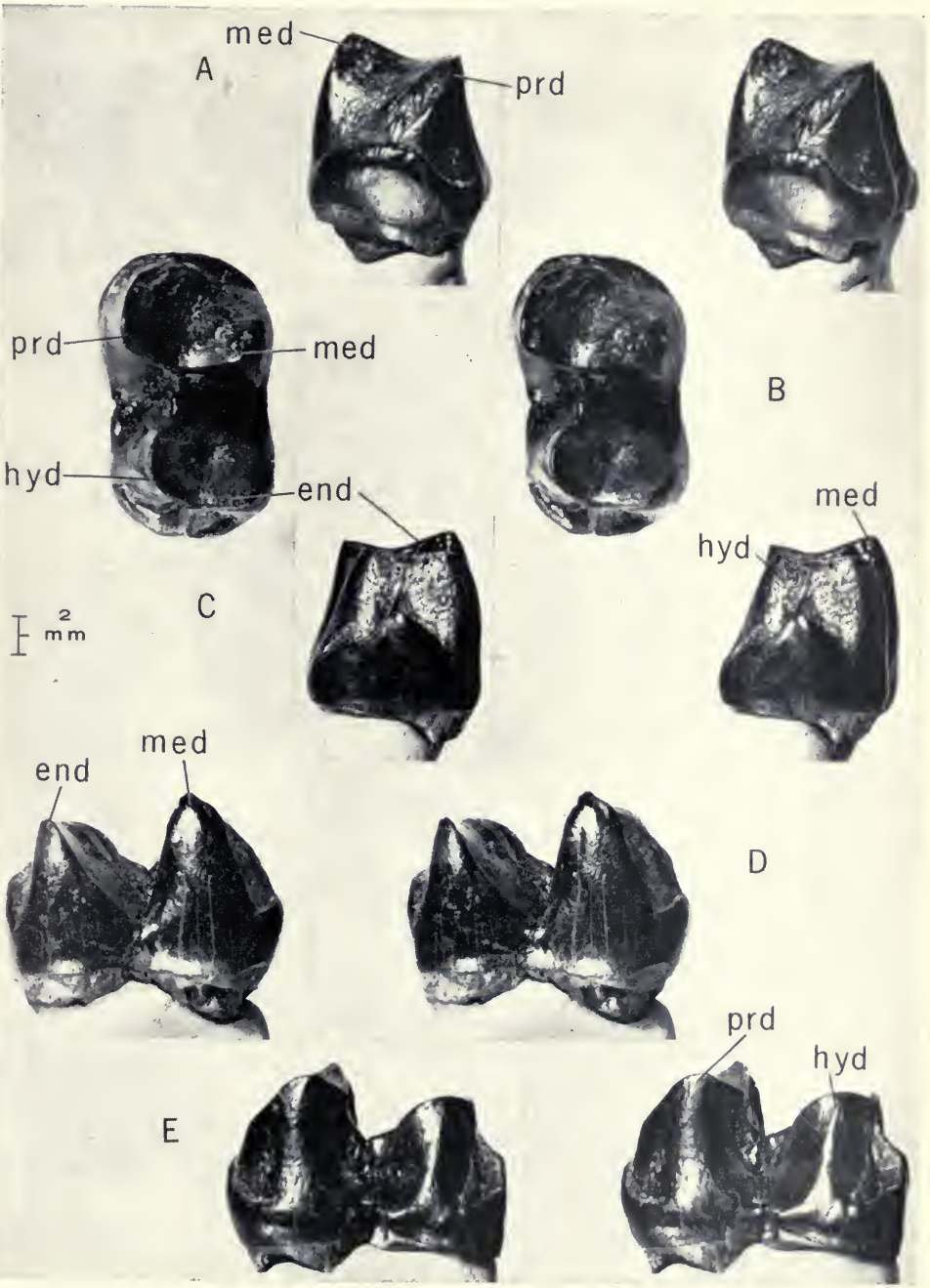
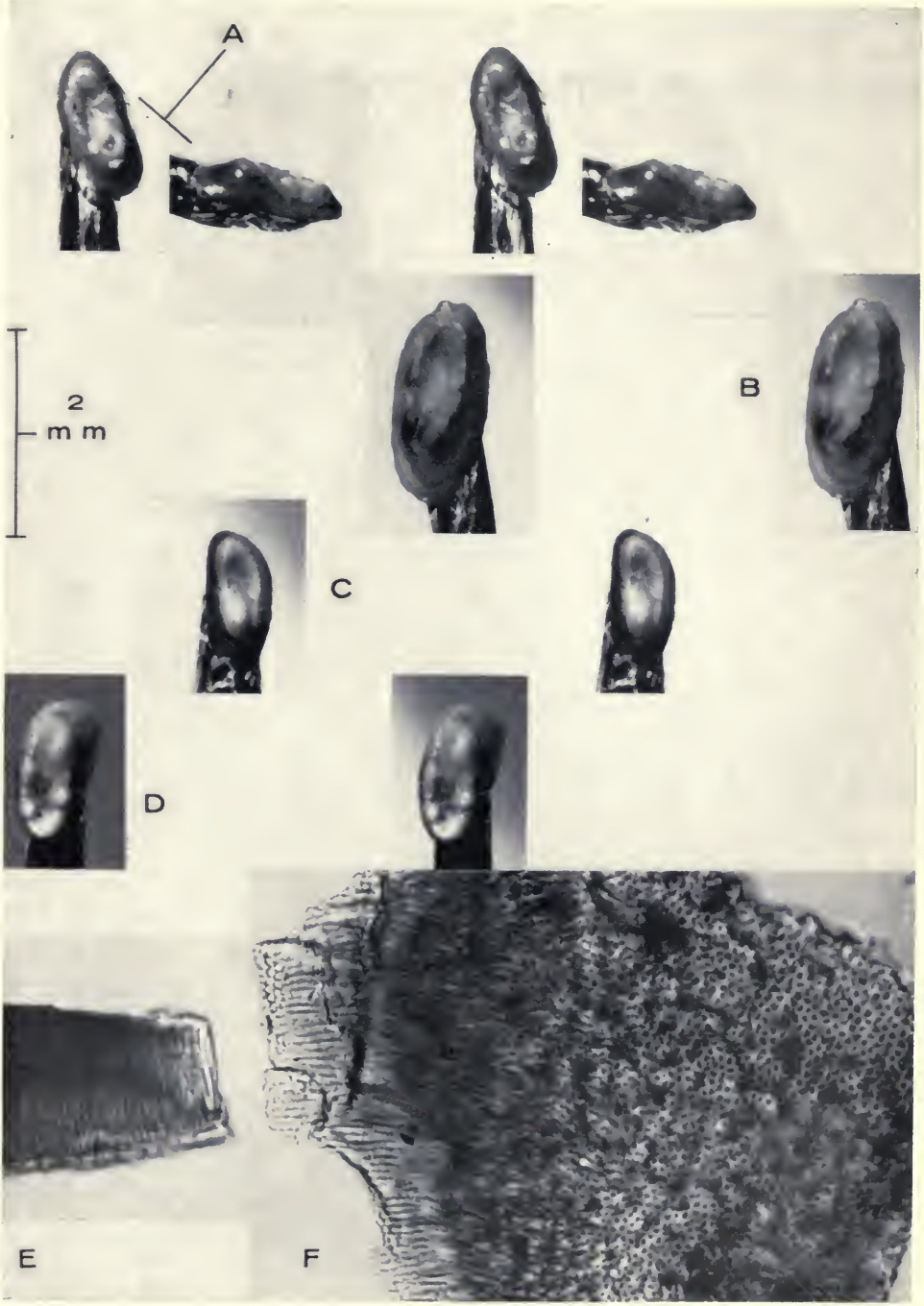
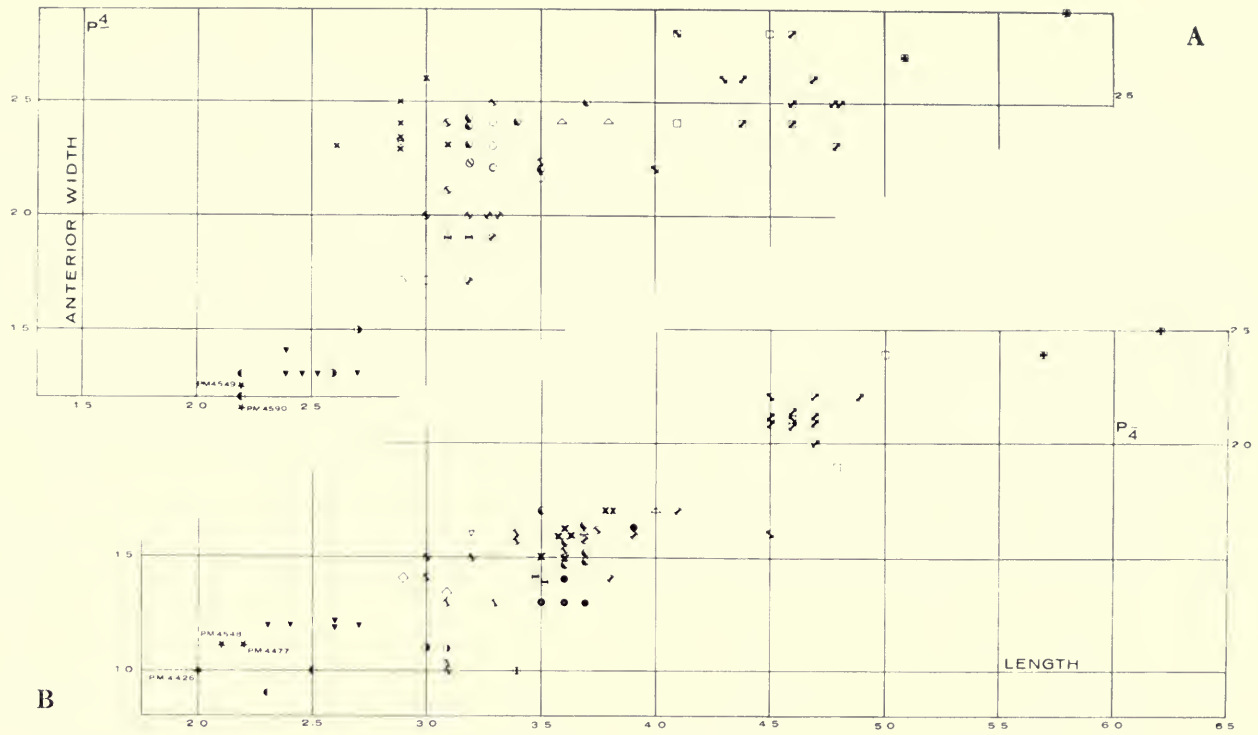

med
A
prd
prd
med
B
hyd
end
med
hyd
C
2
mm
end
med
D
prd
hyd
E

PLATE XXXI.—Five mammal teeth from the Grange Burn, Pliocene, Hamilton fauna are shown. They are indeterminate as to subclass and lower taxonomic levels. **A.** (NMV-P26425), crown and side views; B–D, crown views **B.** PM 4468. **C.** PM 4466. **D.** PM 4465. Scale for A–D approx. × 15. E, F. Photo micrographs of PM 4599, **E** is a X-section showing peculiar enamel prisms cut lengthwise. **F.** A section approximately tangential to surface of the tooth which shows the enamel prisms cut across over most of the field, and cut obliquely, at the extreme left. Scale of E and F approx. × 940.


A
2
m m
B
C
D
E
F

GRAPHS



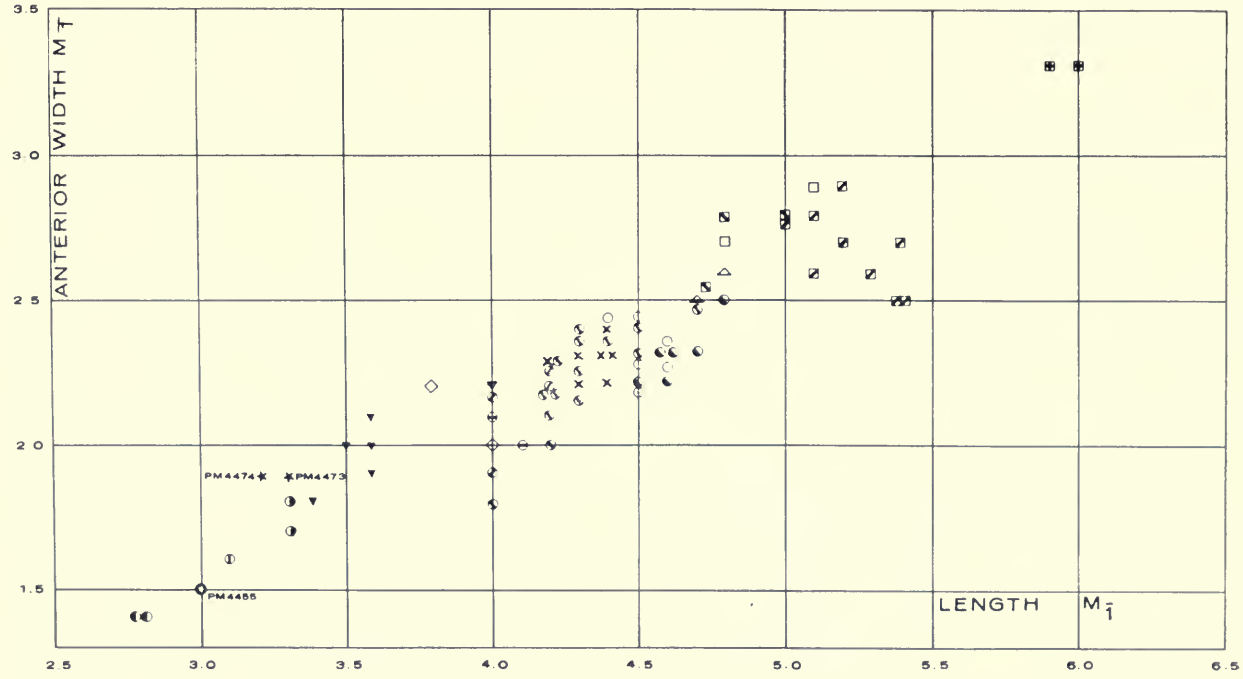
GRAPHS A AND B. —Bivariate plots of length *vs.* anterior width for the P^4 (A) and length *vs.* anterior width for P_4 (B) of several species of pseudocheirines. The position of the Hamilton material shows that in their size and proportions both *Pseudocheirus stirtoni* and *P. marshalli* are similar to the P^4 of *P. pygmaeus* and *Schoinobates volans minor*. Filled circles in Graph B designate *Pseudocheirus convolutus*. In Graphs A, C, D, and E this species is indicated with an open circle. See Graph C for detailed explanation of symbols.

GRAPH C.—Bivariate plot of length *vs.* anterior width of M^1 of various species of pseudocheirines. The position of *Pseudocheirus stirtoni* and *P. marshalli* shows that in the size and proportions of the M^1 they are like the M^1 of *P. pygmaeus*, *P. forbesi*, and *P. canescens* and in contrast to the P^4_4 less like *Schoinobates volans minor*.

GRAPH D.—Bivariate plot of length *vs.* anterior width of M_T of various species of pseudocheirines. The position of *Pseudocheirus stirtoni* and *P. marshalli* indicates that in the proportions of the M_T *P. stirtoni* is similar to *P. forbesi* and *Schoinobates volans minor*, and *P. marshalli* is more similar to *P. pygmaeus* and *P. canescens*.

See Graph C for detailed explanations of symbols.

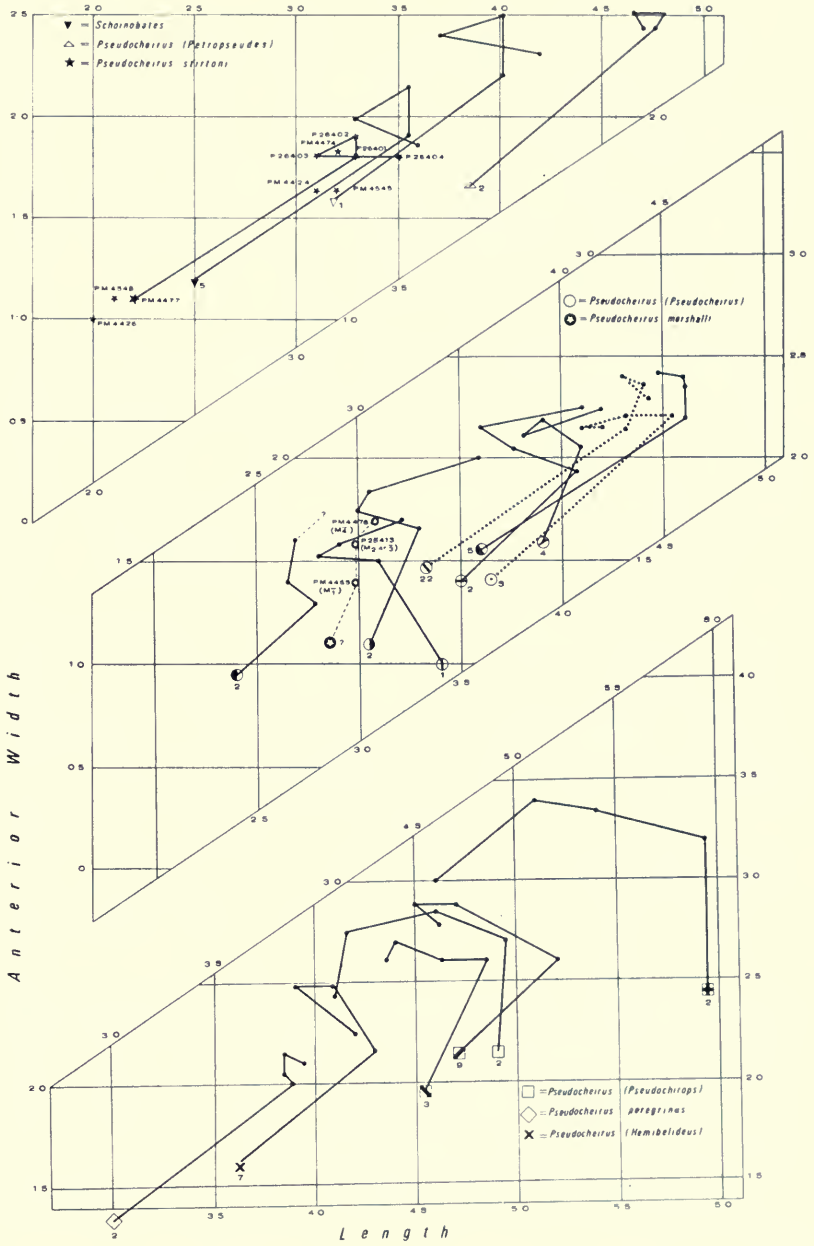
GRAPH D


ANTERIOR WIDTH M$_1$
LENGTH M$_1$
3.5
3.0
2.5
2.0
1.5
2.5
3.0
3.5
4.0
4.5
5.0
5.5
6.0
6.5
PM4474
PM4473
PM4455

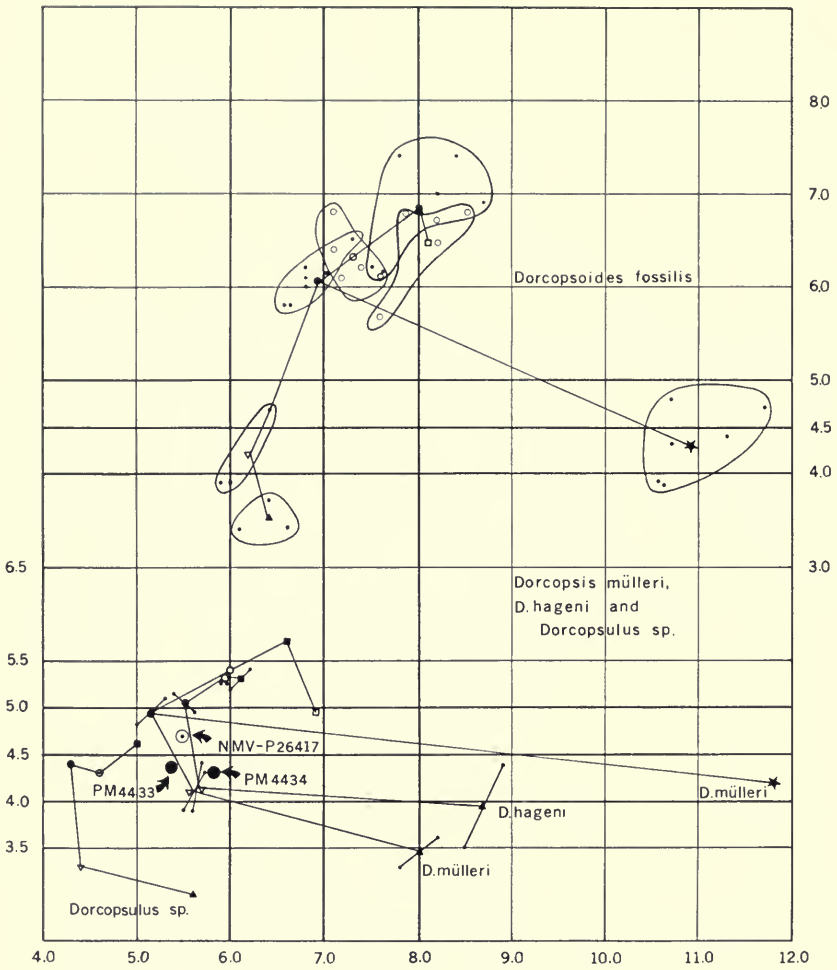
GRAPH E.—Bivariate plots of average dimensions of length *vs.* anterior width of the $P_{\bar{4}}$ through $M_{\bar{1}}$ of various species of pseudocheirines. The symbol for each species appears at the $P_{\bar{4}}$ position and the line extends from there through $M_{\bar{1}}$, $M_{\bar{2}}$, $M_{\bar{3}}$, to $M_{\bar{4}}$. The sample sizes are given adjacent to each species symbol. The plots show graphically the change in proportions of the teeth from anterior to posterior. The resulting patterns are variable but show reasonably consistent patterns at the subgeneric level. The subgenus *Pseudocheirus* consists of two groups of species with different proportions of the $P_{\bar{4}}$ and the $M_{\bar{1}} - M_{\bar{2}}$. The plots show that in the way in which the proportions of the teeth change *P. stirtoni* is similar to *Schoinobates volans minor* and *P. marshalli* is similar to the small-sized group of species in the subgenus *Pseudocheirus* (*P. pygmaeus*, *P. forbesi*, and *P. canescens*).

See Graph C for detailed explanation of the species symbols.

GRAPH E

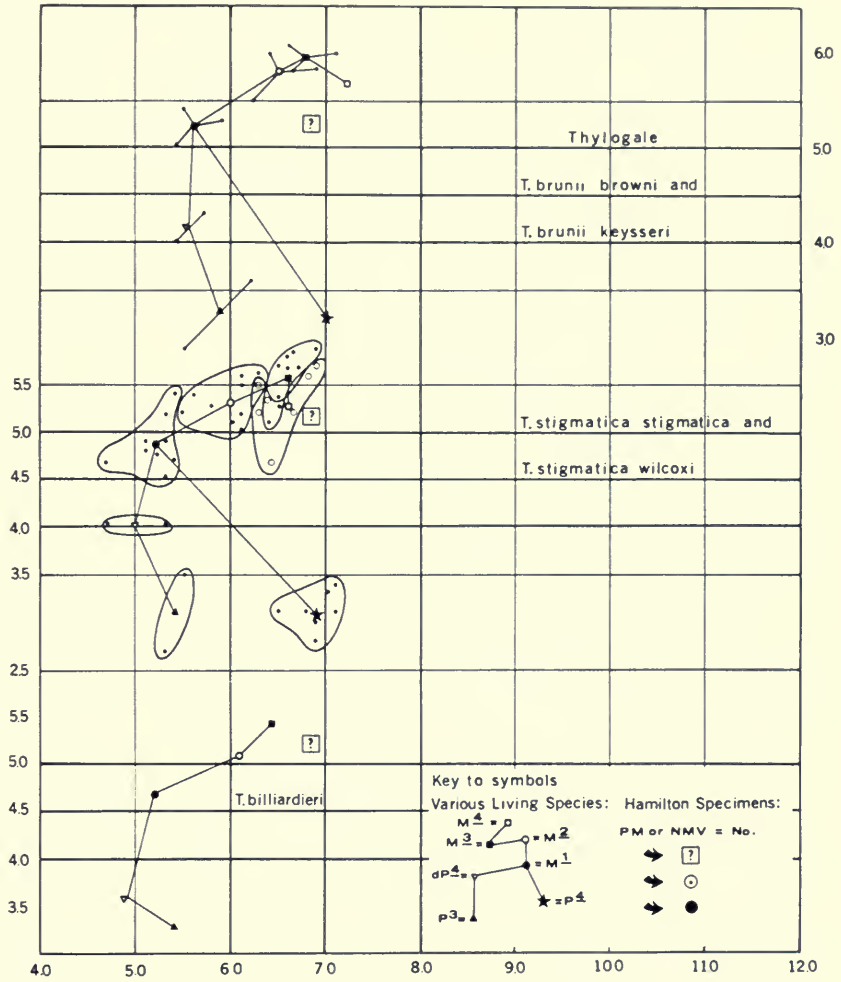

▼ = Schizonbates
△ = Pseudocheirus (Petropseudes)
★ = Pseudocheirus stirtoni
○ = Pseudocheirus (Pseudocheirus)
✪ = Pseudocheirus marshalli
□ = Pseudocheirus (Pseudochirops)
◇ = Pseudocheirus peregrinus
✕ = Pseudocheirus (Hemibelideus)
Anterior Width
Length

GRAPH F

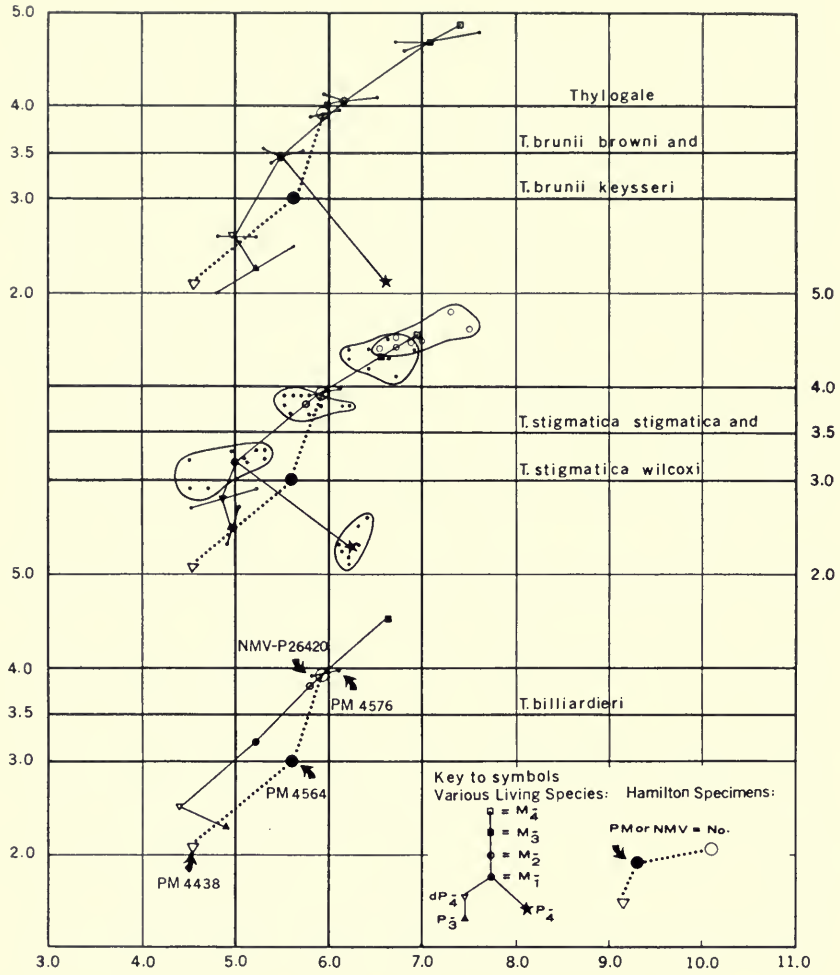


GRAPHS F, G.—Bivariate plots of length (abscissa) *vs.* anterior width (ordinate) of upper cheek teeth of various species of Recent *Dorcopsis*, *Dorcopsulus*, and *Thylogale*, and of the fossil *Dorcopsoides fossilis* compared with those of the Hamilton *Dorcopsis* and *Thylogale* teeth. Key to symbols is shown on G. Tooth symbols are indicated at the joint mean of length and anterior width measures. Point clouds or lines show the dispersion of the samples. The positions of the Hamilton specimens of *Dorcopsis* indicates their closer affinity to the Recent *Dorcopsis* than to either the Recent *Dorcopsulus* or the fossil *Dorcopsoides*. The Hamilton *Thylogale* is similar in size and proportions to the posterior molars of several extant species of *Thylogale*. Discussion is given on pages 60 to 62. *Dorcopsoides* data from Woodburne, 1967.

GRAPH G

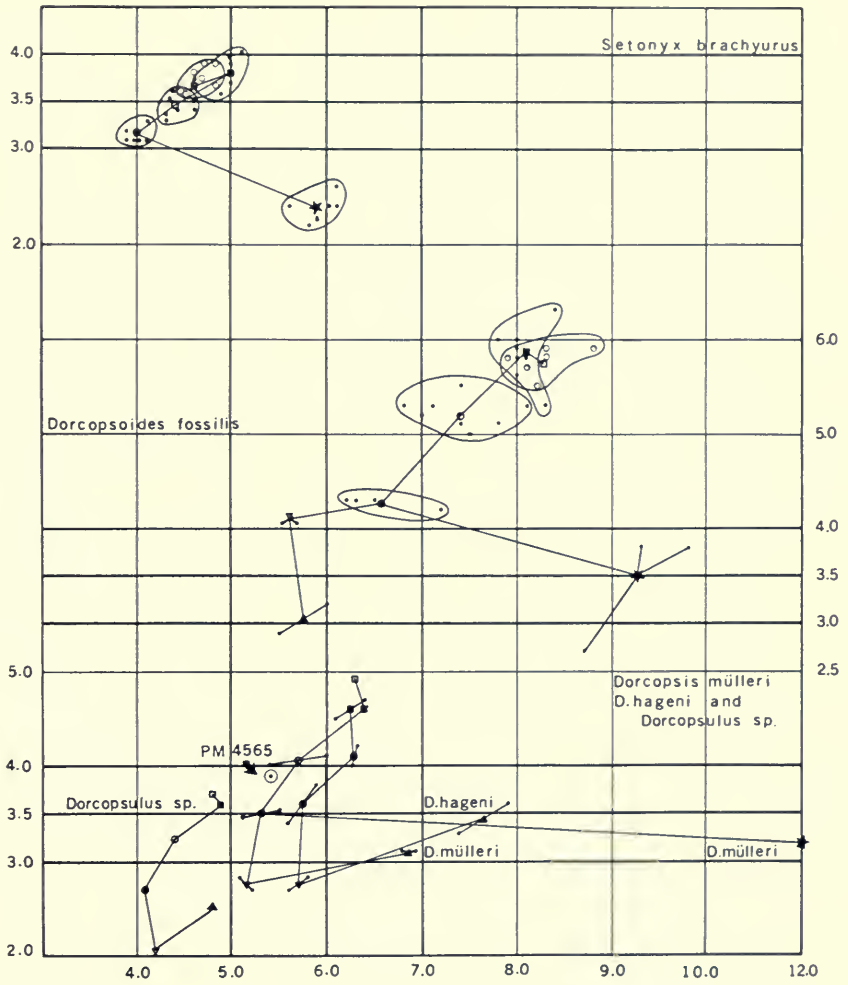

Thylogale
T. brunii browni and
T. brunii keysseri
T. stigmatica stigmatica and
T. stigmatica wilcoxi
T. billiardieri
Key to symbols
Various Living Species:
Hamilton Specimens:
PM or NMV = No.
6.0
5.0
4.0
3.0
5.5
5.0
4.5
4.0
3.5
2.5
5.5
5.0
4.5
4.0
3.5
4.0
5.0
6.0
7.0
8.0
9.0
10.0
11.0
12.0

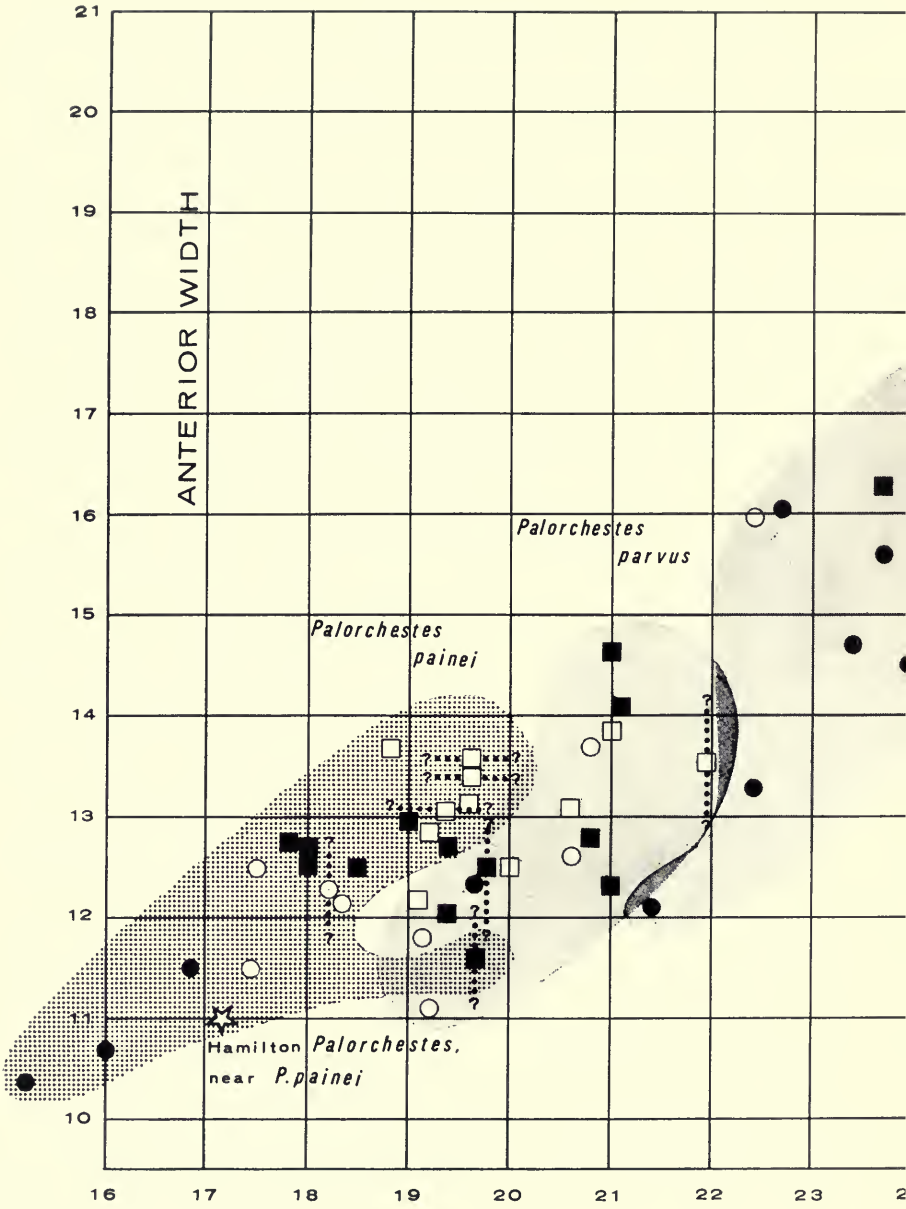
GRAPH H



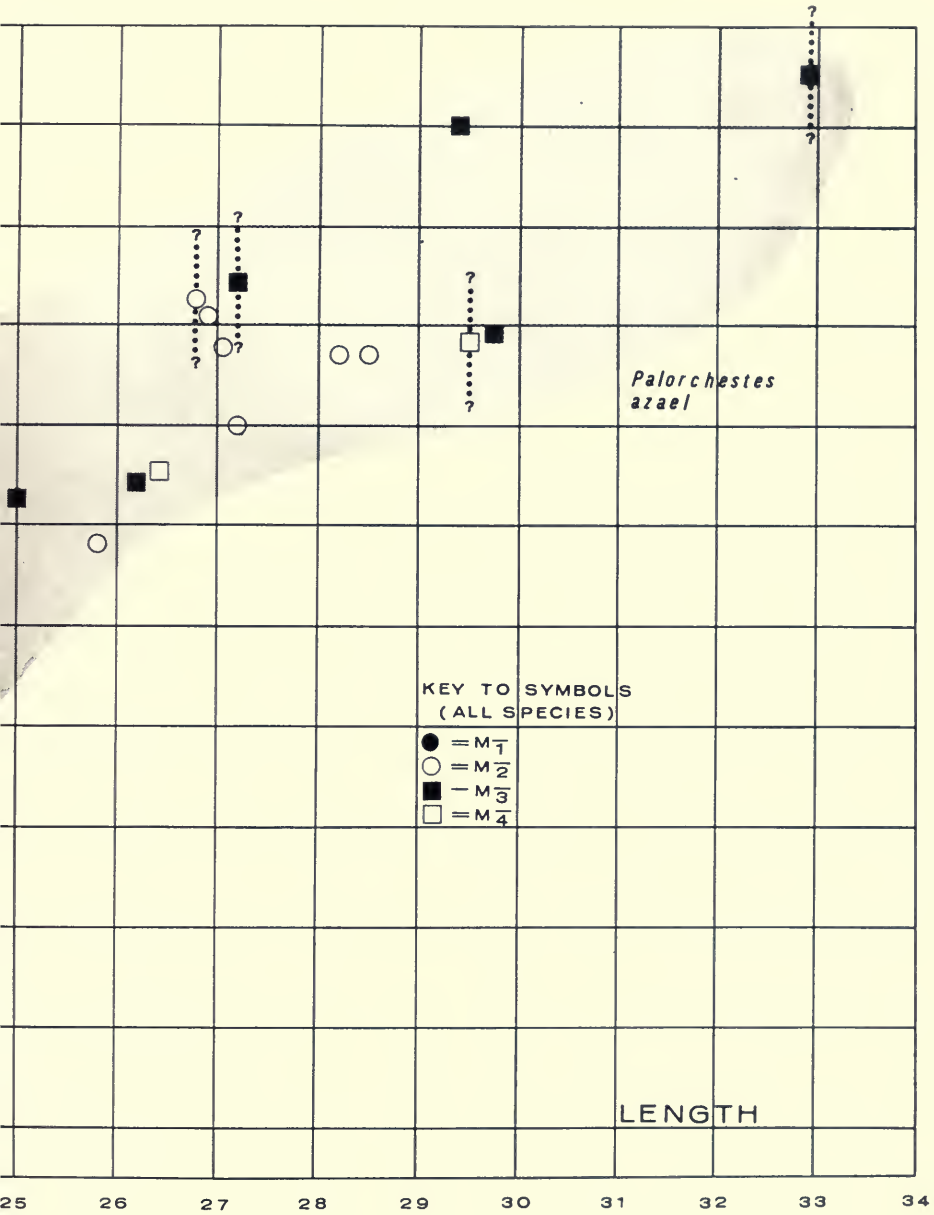
GRAPHS H, I.—Bivariate plots similar to those in F and G, showing length *vs.* anterior width (abscissa and ordinate, respectively) for the lower cheek teeth of the same species samples as shown in F and G. In addition, a sample of Recent *Setonyx* is also shown. The Hamilton *Dorcopsis* and *Thylogale* teeth are plotted for comparison. Symbols are keyed on H, and as further indicated on caption to F. The positions of the Hamilton *Thylogale* specimens indicate that they are all similar in size and proportions to those of several living species of the genus. The Hamilton *Dorcopsis* is most similar in size and proportion to the $M_{\bar{2}}$ of *D. mülleri*. *Dorcopsoides* data from Woodburne, 1967.

GRAPH I


Setonyx brachyurus
Dorcopsoides fossilis
Dorcopsis mülleri
D.hageni and
Dorcopsulus sp.
PM 4565
Dorcopsulus sp.
D.hageni
D.mülleri
D.mülleri
4.0
3.5
3.0
2.0
6.0
5.0
4.0
3.5
3.0
2.5
5.0
4.0
3.5
3.0
2.0
4.0
5.0
6.0
7.0
8.0
9.0
10.0
12.0



GRAPH J.—Bivariate plot of length and anterior width of lower molars of t
species of *Palorchestes*. The Hamilton specimen is clearly similar in size and pr
portions to those of *P. painei*. Most of the data is from Woods (1958).


Palorchestes azael
KEY TO SYMBOLS (ALL SPECIES)
● = M 1
○ = M 2
■ = M 3
□ = M 4
LENGTH
25
26
27
28
29
30
31
32
33
34

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